

Deceiving Others: Distinct Neural Responses of the Prefrontal Cortex and Amygdala in Simple Fabrication and Deception with Social Interactions

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Abstract

■ Brain mechanisms for telling lies have been investigated recently using neuroimaging techniques such as functional magnetic resonance imaging and positron emission tomography. Although the advent of these techniques has gradually enabled clarification of the functional contributions of the prefrontal cortex in deception with respect to executive function, the specific roles of subregions within the prefrontal cortex and other brain regions responsible for emotional regulation or social interactions during deception are still unclear. Assuming that the processes of falsifying truthful responses and deceiving others are differentially associated with the activities of these regions, we conducted a positron emission tomography experiment with 2 (truth, lie) × 2 (honesty, dishonesty) factorial design. The main effect of falsifying the truthful re-

sponses revealed increased brain activity of the left dorsolateral and right anterior prefrontal cortices, supporting the interpretation of previous studies that executive functions are related to making untruthful responses. The main effect of deceiving the interrogator showed activations of the ventromedial prefrontal (medial orbitofrontal) cortex and amygdala, adding new evidence that the brain regions assumed to be responsible for emotional processing or social interaction are active during deceptive behavior similar to that in real-life situations. Further analysis revealed that activity of the right anterior prefrontal cortex showed both effects of deception, indicating that this region has a pivotal role in telling lies. Our results provide clear evidence of functionally dissociable roles of the prefrontal subregions and amygdala for human deception. ■

INTRODUCTION

Since the pioneering research of Spence et al. (2001), an increasing number of neuroimaging studies have shown contributions of the prefrontal cortex to deception (Abe et al., 2006; Mohamed et al., 2006; Davatzikos et al., 2005; Kozel et al., 2005; Langleben et al., 2005; Lee et al., 2005; Nunez, Casey, Egner, Hare, & Hirsch, 2005; Phan et al., 2005; Kozel, Padgett, & George, 2004; Kozel, Revell, et al., 2004; Ganis, Kosslyn, Stose, Thompson, & Yurgelun-Todd, 2003; Langleben et al., 2002; Lee et al., 2002). Although subregions of this area have been differentially activated in these studies, their precise roles in relation to deception are still unclear.

Previous neuroimaging studies of deception have focused on the truthfulness of responses as an essential factor (simple fabrication, i.e., the inhibition of true responses and the production of deceptive ones). However, the reported activations of the prefrontal cortex might not be solely associated with processes of falsifying responses, because deception is not a simple mental

activity, but rather a complex one composed of various cognitive functions. Although the inhibition of true responses and the production of deceptive ones are prerequisites for deception, the intention of deceiving others (deception with social interactions, i.e., deluding a questioner, irrespective of whether a response is truthful), which is likely to be accompanied by emotional regulation or social interaction, must be regarded as another important determinant for human deception.

There is a growing body of evidence for dissociable functional specialization of subregions within the prefrontal cortex from previous neuropsychological, neuroimaging, and animal studies (Fuster, 2001). Above all, in relation to deception, it is worthwhile noting that the lateral (especially dorsolateral) prefrontal cortex is associated with executive function and the medial (especially ventromedial) prefrontal cortex with emotional regulation or social interaction (Mesulam, 2000).

In the present positron emission tomography (PET) study, we used a novel task paradigm to test directly our hypothesis that during the telling of lies, the lateral prefrontal cortex would be associated with the processes of inhibition of true responses and production of deceptive ones, and the medial prefrontal cortex would

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be associated with the intention of deceiving an interrogator. Based on the findings of previous studies (Abe et al., 2006; Mohamed et al., 2006; Kozel et al., 2005; Lee et al., 2005; Nunez et al., 2005; Kozel, Padgett, et al., 2004; Kozel, Revell, et al., 2004; Ganis et al., 2003; Langleben et al., 2002), involvement of the anterior cingulate cortex related to the inhibition of true responses and the production of deceptive responses would also be posited. In addition, activity of the amygdala crucial for emotional processing (Dolan, 2002; LeDoux, 2000) would be expected in relation to the intention of deceiving the interrogator. During PET scanning, participants performed a series of deception tasks determined by two discrete factors: the truthfulness of responses and the intention of deceiving the interrogator. Our results underscore an essential aspect of human deceptive behavior that has never been explored and provide clear evidence that at least two factors essential for human deception are supported by distinct subregions within the prefrontal cortex.

METHODS

Participants

Sixteen male volunteers who had no history of neurological or psychiatric disease were paid to take part in this study (mean age = 20.3 years, range = 18–22 years). There were no pathological findings on magnetic resonance imaging (MRI) of any of the subjects' brains. All of the subjects were right-handed on the Edinburgh Handedness Inventory (Oldfield, 1971). The subjects gave their written informed consent in accordance with the Declaration of Helsinki, and the guidelines were approved by the Ethical Committee of Tohoku University.

Stimuli

For the deception tasks during PET scanning, we prepared 48 questions related to autobiographical semantic memory (e.g., "What is the name of your primary school?" "Who is your best friend in junior high school?"). These questions included 16 on primary school life, 16 on junior high school life, and 16 on high school life. They were divided into four lists, each consisting of 12 stimuli (four questions per school period).

Tasks

During PET imaging, the subjects performed the following four tasks (Figure 1). (1) Honest–truth (HT) task: Subjects were instructed by the interrogator to tell the truth about their past memories. (2) Honest–lie (HL) task: Subjects were instructed by the interrogator to tell lies about their past memories. (3) Dishonest–truth (DT) task: Subjects were instructed by the interrogator to tell lies about their past memories, but approximately 2 min before the initiation of this task, another exper-

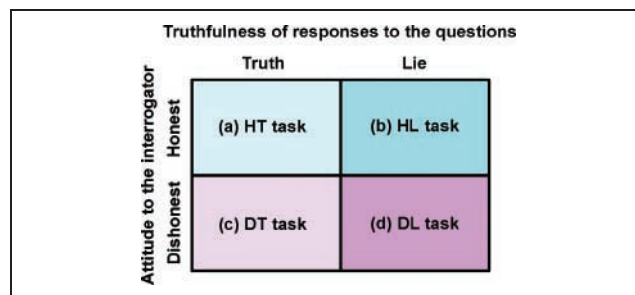


Figure 1. Schematic of deception tasks in the present study.

Conditions were varied as a function of the truthfulness of responses (truth vs. lie) and of attitude to the interrogator (honest vs. dishonest). (a) HT task: The participants obeyed the interrogator and told the truth in response to questions. (b) HL task: The participants obeyed the interrogator and told lies in response to questions. (c) DT task: The participants deceived the interrogator and told the truth in response to questions. (d) DL task: The participants deceived the interrogator and told lies in response to questions.

imenter (the second experimenter) secretly asked the subjects to deceive the interrogator by answering the questions truthfully. (4) Dishonest–lie (DL) task: Subjects were instructed by the interrogator to tell the truth about their past memories, but approximately 2 min before the initiation of this task, the second experimenter secretly asked the subjects to deceive the interrogator by answering the questions untruthfully. In these four tasks, the use of the four lists of questions related to autobiographical semantic memory was counterbalanced across the subjects. The order of the four tasks was also counterbalanced across the subjects.

Before the transmission scan, the interrogator explained to the subjects that they had to perform four tasks and that they had to give untruthful answers in response to the questions in two of the tasks. Just before the initiation of the four tasks, the interrogator instructed the subjects to tell the truth in the HT and DL tasks and to tell lies in the HL and DT tasks. During approximately 10-min breaks between the tasks, which were required for sufficient decay of the radioactive tracers, the interrogator always left the experiment room, while the second experimenter and the subject remained in the room. Before the DL and DT conditions, respectively, during these breaks, the second experimenter asked the subjects to deceive the interrogator by telling lies or the truth about the presented questions. The subjects were also told that the interrogator did not know he would be deceived and that deceiving the interrogator was the most important purpose of the study. Furthermore, subjects were asked to make sure that the interrogator did not discover the study's real purpose.

To elucidate the neural basis of deception associated with this factor of intention to deceive the interrogator, we made the experimental setting as close to a real-life situation as possible. First, we used PET, but not functional MRI (fMRI), because of the latitude of PET in terms

of direct communication between subjects and experimenters. Second, the questions about autobiographical semantic memory were presented using the interrogator's voice approximately every 7.5 sec. Third, the form of the subjects' responses was not a yes/no button press, but a one-word verbal answer.

After PET imaging was completed, the subjects were told that the interrogator had been aware of the true facts of the experimental procedure (i.e., that the subjects had tried to deceive him). Subjects were also debriefed with regard to their senses of sin (i.e., feelings of immorality) and anxiety (i.e., feelings of impatience and stress) during the four tasks to assess the validity of the study's experimental paradigm. The senses of sin and anxiety were rated from 1 (*very strong feeling*) to 4 (*very weak feeling*). In addition, to evaluate the accuracy of the subjects' task performance, they were again presented with the 48 questions used during PET scanning and asked to give the correct answers.

Data Acquisition

All the interrogator's questions and the subjects' oral responses were recorded on a digital sound recording machine. These data were subsequently used for the evaluation of performance accuracy and reaction times.

Regional cerebral blood flow (rCBF) was measured using PET (SET2400W Shimadzu, Kyoto, Japan; full width at half maximum = 4.0 mm) and ^{15}O -labeled water (approximately 180 MBq for each injection). The transaxial sampling field of view was 256 mm, and the axial field of view was 190 mm. The thickness of the slices measured was 3.125 mm. Before the PET experiments, a catheter was inserted into the subject's right brachial vein for tracer administration, and the subject's head was fixed to an air-cushioned headrest apparatus. Each PET data acquisition time was 60 sec, and the start of the acquisition was 15 sec after the start of each task. A transmission scan was followed by the experiment, and the data were used to obtain corrected emission images. A T1-weighted MRI image (1.5 T) was obtained on a separate occasion for coregistration in spatial preprocessing.

Data Analysis

The PET data were analyzed with SPM2 (Wellcome Department of Imaging Neuroscience, London, UK). All rCBF images were realigned to correct for small movements between scans. A T1-weighted structural MRI was coregistered to the mean image of realigned PET images. Then, the coregistered T1 image was normalized to the Montreal Neurological Institute (MNI) template. Using the parameters from this normalization process, the PET images were also reformatted to isometric voxels ($2 \times 2 \times 2$ mm) and smoothed with a 10-mm full width at half maximum Gaussian kernel. The rCBF-equivalent measurements were

adjusted to a global CBF mean of 50 ml/dl/min. Contrast of the main effect of each voxel was assessed using t statistics, resulting in a statistical image. In this SPM whole-brain analysis, the threshold of significance was set at $p < .001$ (uncorrected for multiple comparisons), with the extent threshold of 15 contiguous voxels. Then, we extracted the rCBF values of the maximally activated voxel of the observed activations during all the task conditions of each subject and analyzed using two-way analysis of variance (ANOVA), with truthfulness of responses (truth, lie) and intention of deceiving the interrogator (honesty, dishonesty) as factors. Except for SPM whole-brain analysis, the threshold of statistical significance in all of the analyses was set at $p < .05$.

RESULTS

Behavioral Data

All the behavioral data are shown in Table 1. The mean accuracy and reaction times were 87.2% and 1403 msec, respectively, for the HT task, 88.0% and 1686 msec, respectively, for the HL task, 82.8% and 1785 msec, respectively, for the DT task, and 82.3% and 1783 msec, respectively, for the DL task. These data were analyzed using two-way repeated measures ANOVA, with the truthfulness of responses (truth, lie) and the intention of deceiving the interrogator (honesty, dishonesty) as factors. In the analysis of performance accuracy, ANOVA showed a significant main effect of the intention of deceiving the interrogator [$F(1,15) = 6.945, p < .05$], but showed neither a main effect of the truthfulness of responses [$F(1,15) = 0.001, p = .973$] nor an interaction between the two factors [$F(1,15) = 0.074, p = .789$]. ANOVA for the data of reaction times showed a significant main effect of the intention of deceiving the interrogator [$F(1,15) = 5.073, p < .05$] and a noticeable trend of main effect of the truthfulness of responses [$F(1,15) = 4.469, p = .052$], without an interaction [$F(1,15) = 2.192, p = .160$].

The mean scores of ratings for senses of sin and anxiety during the four conditions were 4.0 and 3.8 for the HT task, 3.8 and 3.6 for the HL task, 3.4 and 2.6 for the DT task, and 3.3 and 1.9 for the DL task. A Friedman test revealed significant differences in the senses of both sin ($p < .001$) and anxiety ($p < .001$). For the sense of sin, a post hoc analysis using a Wilcoxon signed rank test

Table 1. Behavioral Data during Four Tasks (Mean \pm SD)

Task	Percent Correct	Reaction Time (msec)	Sense of Sin	Sense of Anxiety
HT	87.2 \pm 9.1	1403 \pm 493	4.0 \pm 0.0	3.8 \pm 0.4
HL	88.0 \pm 15.8	1685 \pm 802	3.8 \pm 0.4	3.6 \pm 0.7
DT	82.8 \pm 12.4	1785 \pm 549	3.4 \pm 0.8	2.6 \pm 1.0
DL	82.3 \pm 13.9	1783 \pm 535	3.3 \pm 0.8	1.9 \pm 0.9

with Bonferroni correction revealed a significant difference only between the HT and DL tasks ($p = .006$). For anxiety, a post hoc analysis revealed three significant differences: one between the HT and DT tasks ($p = .004$), another between the HL and DL tasks ($p = .001$), and the other between the HT and DL tasks ($p = .001$).

Brain Activation

First, to identify the brain regions associated with the two factors of deception, main effects of each factor were calculated from the functional imaging data. The main effect of falsifying the truthful responses $\{(HL - HT) + (DL - DT)\}$ revealed significant activations in the left dorsolateral prefrontal cortex (Brodmann's area [BA] 8/9), left precuneus (BA 7), left cerebellum, right anterior prefrontal cortex (BA 10), and right cuneus (subcortical). The main effect of deceiving the interrogator $\{(DT - HT) + (DL - HL)\}$ revealed significant activations in the left ventromedial prefrontal cortex (BA 11), left precuneus (subcortical), left cerebellum, right middle temporal gyrus (BA 38), right inferior temporal gyrus (BA 20/38), and right cerebellum. At this stage of the analysis, setting a more lenient threshold ($p < .005$, cluster size > 15), we further examined whether the anterior cingulate cortex and the amygdala showed increased activity in either main effect. In the main effect of deceiving the interrogator, activation was detected in the left amygdala. No significant activation was found in

the anterior cingulate cortex. Table 2 summarizes the data for anatomical structures and BA, MNI coordinates, Z values, and cluster sizes of peak activations.

Second, to elucidate whether each main effect and an interaction were significant in the five regions detected in the main effect of lie and the seven regions in the main effect of dishonest, the rCBF values extracted from the activation peak for each region were analyzed using two-way ANOVA, with truthfulness of responses (truth, lie) and intention of deceiving the interrogator (honesty, dishonesty) as factors.

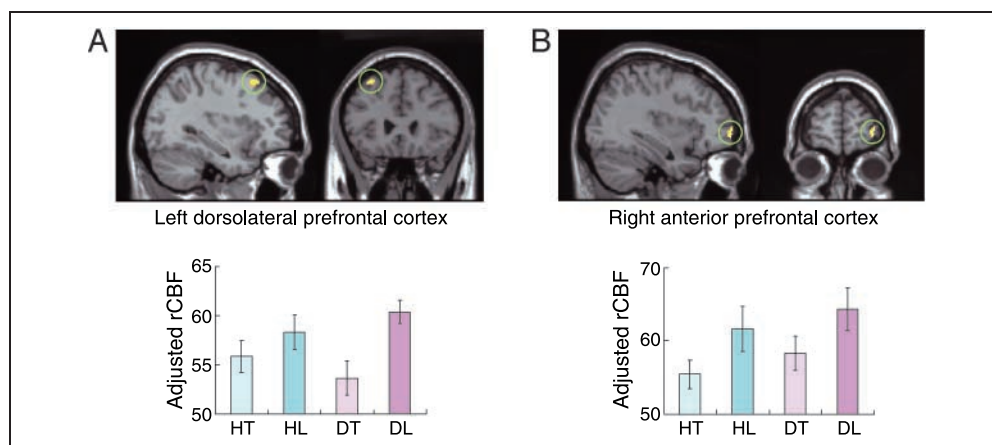
As for the regions detected in the main effect of falsifying the truthful responses, the right anterior prefrontal cortex showed significant main effects of lie [$F(1,15) = 12.642, p < .005$] and dishonesty [$F(1,15) = 12.141, p < .005$], without an interaction [$F(1,15) = 0.004, p = .953$]. The left dorsolateral prefrontal cortex showed a significant main effect of lie [$F(1,15) = 12.388, p < .005$], without a main effect of honesty/dishonesty [$F(1,15) = 0.003, p = .955$] or an interaction [$F(1,15) = 2.901, p = .109$]. The remaining three regions showed the same statistical patterns as the left dorsolateral prefrontal cortex [left precuneus: main effect of lie, $F(1,15) = 13.582, p < .005$; main effect of honesty/dishonesty, $F(1,15) = 2.795, p = .115$; interaction, $F(1,15) = 0.017, p = .897$; left cerebellum: main effect of lie, $F(1,15) = 34.399, p < .0001$; main effect of honesty/dishonesty, $F(1,15) = 0.551, p = .469$; interaction, $F(1,15) = 0.634, p = .438$; right cuneus (subcortical): main effect of lie, $F(1,15) = 19.218, p < .005$].

Table 2. Brain Regions Showing Activation in Each Main Effect of Deception

Region (BA)	MNI Coordinates			Z Value	Cluster Size
	x	y	z		
<i>Main effect of falsifying the truthful responses $\{(HL - HT) + (DL - DT)\}$</i>					
Left dorsolateral prefrontal cortex (8/9)	-32	26	56	3.49	24
Left precuneus (7)	-12	-60	50	3.64	34
Left cerebellum	-10	-72	-28	4.53	48
Right anterior prefrontal cortex (10)	36	62	-2	4.11	19
Right cuneus (subcortical)	26	-70	14	3.74	22
<i>Main effect of deceiving the interrogator $\{(DT - HT) + (DL - HL)\}$</i>					
Left ventromedial prefrontal cortex (11)	-2	42	-16	3.93	18
Left precuneus (subcortical)	-14	-56	42	3.59	22
Left cerebellum	-14	-74	-48	3.54	29
Left amygdala*	-26	0	-26	2.95	24
Right middle temporal gyrus (38)	34	12	-34	3.96	53
Right inferior temporal gyrus (20)	50	8	-40	3.86	20
Right cerebellum	34	-54	-42	3.47	18

All peaks, $p < .001$, uncorrected, except * $p < .005$.

Figure 2. Activations of (A) the left dorsolateral prefrontal cortex and (B) the right anterior prefrontal cortex detected in a main effect of falsifying the truthful responses (lie) in SPM analysis. The activations are superimposed onto MRIs of MNI templates ($p < .005$ for a display purpose). Histogram bars represent the rCBF values (mean \pm SEM) adjusted by global normalization during the four tasks. The left dorsolateral prefrontal cortex showed a main effect of lie only, whereas the right anterior prefrontal cortex showed main effects of both lie and dishonesty.



.001; main effect of honesty/dishonesty, $F(1,15) = 0.304$, $p = .590$; interaction, $F(1,15) = 2.750$, $p = .118$]. The results of the right anterior and left dorsolateral prefrontal cortices are illustrated in Figure 2.

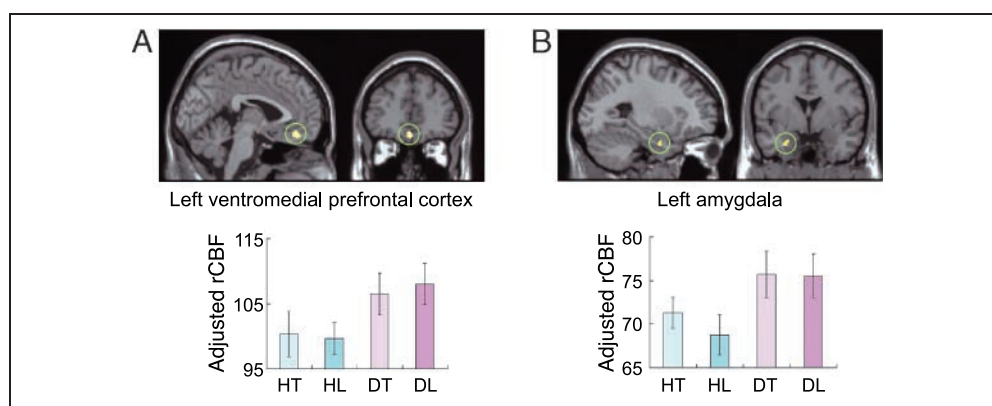
As for the regions detected in the main effect of deceiving the interrogator, the left precuneus (subcortical) showed a significant main effect of dishonesty [$F(1,15) = 15.078$, $p < .005$] and a trend of main effect of lie [$F(1,15) = 3.156$, $p = .096$], without an interaction [$F(1,15) = 0.942$, $p = .347$]. The right middle temporal gyrus showed significant main effects of dishonesty [$F(1,15) = 10.547$, $p < .01$] and truth [$F(1,15) = 17.399$, $p < .001$], with a trend of interaction [$F(1,15) = 4.034$, $p = .063$]. The left ventromedial prefrontal cortex showed a significant main effect of dishonesty [$F(1,15) = 18.622$, $p < .001$], without a main effect of truth/lie [$F(1,15) = 0.100$, $p = .756$] or an interaction [$F(1,15) = 0.326$, $p = .577$]. The left amygdala showed a significant main effect of dishonesty [$F(1,15) = 9.964$, $p < .01$], without a main effect of truth/lie [$F(1,15) = 0.505$, $p = .489$] or an

interaction [$F(1,15) = 0.504$, $p = .489$]. The remaining three regions showed the same patterns as the left ventromedial prefrontal cortex and amygdala [right inferior temporal gyrus: main effect of dishonesty, $F(1,15) = 12.607$, $p < .005$; main effect of truth/lie, $F(1,15) = 0.553$, $p = .469$; interaction, $F(1,15) = 0.438$, $p = .518$; left cerebellum: main effect of dishonesty, $F(1,15) = 13.123$, $p < .005$; main effect of truth/lie, $F(1,15) = 2.270$, $p = .153$; interaction, $F(1,15) = 1.763$, $p = .204$; right cerebellum: main effect of dishonesty, $F(1,15) = 14.954$, $p < .005$; main effect of truth/lie, $F(1,15) = 0.976$, $p = .339$; interaction, $F(1,15) = 0.625$, $p = .442$]. The results of the left ventromedial prefrontal cortex and amygdala are illustrated in Figure 3.

DISCUSSION

The main purpose of the present study was to clarify further the functional dissociation within the prefrontal

Figure 3. Activations of (A) the left ventromedial prefrontal cortex and (B) the left amygdala detected in a main effect of deceiving the interrogator (dishonesty) in SPM analysis. The activations are superimposed onto MRIs of MNI templates ($p < .005$ for a display purpose). Histogram bars represent the rCBF values (mean \pm SEM) adjusted by global normalization during the four tasks. The ventromedial prefrontal cortex and amygdala showed a main effect of dishonesty without the other main effect and an interaction.



cortex during deception. In addition to the truthfulness of responses, the novel factor of deceiving the interrogator was also manipulated. Based on the previous findings of studies related to emotional regulation or social interaction as well as deception itself, our primary focus was not only on the activity of subregions within the prefrontal cortex but also on activity in the anterior cingulate cortex and the amygdala. The functional imaging data revealed that the left dorsolateral and right anterior prefrontal cortices were associated with the process of falsifying the truthful responses, whereas the left ventromedial prefrontal cortex and amygdala were associated with the process of deceiving the interrogator. Further analysis showed that the right anterior prefrontal cortex was associated with both factors of deception. Critically, our results provide direct evidence for dissociable brain activities of prefrontal subregions and amygdala in relation to the two different factors of deception.

The behavioral data showed that we achieved our aim of making the task situation for deception close to real life. The mean accuracy and reaction times showed a significant main effect of dishonesty, suggesting that the process of deceiving the interrogator might make more cognitive demands than that of obeying the interrogator. In addition, the rating scores for the senses of sin and anxiety during the four tasks provided support for the validity of the present experimental paradigm.

Consistent with the results of previous studies showing evidence of significant contributions of the lateral prefrontal cortex to deception (Abe et al., 2006; Mohamed et al., 2006; Davatzikos et al., 2005; Kozel et al., 2005; Langleben et al., 2005; Lee et al., 2005; Nunez et al., 2005; Phan et al., 2005; Kozel, Padgett, et al., 2004; Kozel, Revell, et al., 2004; Ganis et al., 2003; Langleben et al., 2002; Lee et al., 2002; Spence et al., 2001), increased brain activities of the left dorsolateral and right anterior prefrontal cortices were found in the conventional analysis of the main effect of falsifying the truthful responses. Activations of the lateral prefrontal cortices related to the inhibition of true responses and the production of deceptive ones are likely to reflect executive function such as working memory and cognitive control (Duncan, 2001; Miller & Cohen, 2001). The behavioral data showing longer reaction times with a noticeable trend of main effect of lie, which would be associated with an interference effect of response inhibition, might also support this interpretation.

Another possible interpretation for the left dorsolateral prefrontal activity is that this region might be associated with the processes of word finding (Phelps, Hyder, Blamire, & Shulman, 1997; Frith, Friston, Liddle, & Frackowiak, 1991), because the subjects' responses were not in the form of yes/no button pressings, but were open-ended verbal responses that required ability similar to that of verbal fluency for the search for appropriate (untruthful) responses in the HL and DL tasks. There is also another possible interpretation for the right

anterior prefrontal activity. This activity might reflect an elevated cognitive load in episodic memory retrieval in the process of falsifying the truthful responses, because the subjects had to retrieve their past experiences more correctly and quickly for the next process of making deceptive responses. Consistent with this interpretation, the activation of right anterior prefrontal cortex has been shown to be tied closely to successful memory retrieval (Herron, Henson, & Rugg, 2004; Rugg, Henson, & Robb, 2003; Henson, Rugg, Shallice, & Dolan, 2000; McDermott, Jones, Petersen, Lageman, & Roediger, 2000).

Interestingly, the right anterior prefrontal cortex was further identified as being important for the two factors of deception—falsifying truthful responses and deceiving the interrogator. Considering the nature of human deception, which is one of the highest order mental activities requiring multiple cognitive processes (Spence et al., 2004), there is a possibility that this region might play a pivotal role in deception with respect not only to executive function (e.g., MacLeod, Buckner, Miezin, Petersen, & Raichle, 1998), but also to social cognition or the integration of the two. In fact, damage to the anterior prefrontal cortex in addition to the ventromedial prefrontal cortex has been reported to cause specific deficits in social behaviors such as everyday planning, decision making, and reasoning (Damasio, Tranel, & Damasio, 1991; Shallice & Burgess, 1991). In a comprehensive review of anatomical and functional neuroimaging studies, Ramnani and Owen (2004) argued that the anterior prefrontal cortex plays a role in integrating the outcomes of two or more separate cognitive operations in the pursuit of a higher behavioral goal. In addition, Keenan, Rubio, Racioppi, Johnson, and Barnacz (2005) argued in their review of the literature that the right hemisphere appears dominant for tasks involving deception. Collectively, our results and those of these previous studies suggest that the right anterior prefrontal cortex might be substantially involved in telling lies.

In the main effect of deceiving the interrogator, another essential aspect of human deception, the left amygdala and ventromedial prefrontal (medial orbitofrontal) cortex were found to be active. This result might be related to the previous findings that both the amygdala and ventromedial prefrontal cortex are associated with emotional processing (Adolphs, Tranel, & Damasio, 2001). Although recent studies have explored the neural activities of deceived subjects and found activation of the amygdala (Grezes, Berthoz, & Passingham, 2006; Grezes, Frith, & Passingham, 2004), no previous studies focusing on the neural activities of those telling lies have detected activation of the amygdala. In the present study, our experimental paradigm with the new factor of deceiving the interrogator might have encouraged the subjects to activate the emotional aspect during deceptive behaviors, and therefore activation of the amygdala could be barely detected ($p < .005$). This interpretation

is plausible, because the increased amygdala activity was accompanied by a higher sense of anxiety (relatively negative emotion in our tasks) in the two conditions of deceiving the interrogator. Alternatively, in the context of deceiving the interrogator, the subjects might have interpreted the questions presented by the interrogator as threats, which might have elicited activation of the amygdala. Consistent with these interpretations, some previous neuroimaging studies have provided evidence supporting a relationship between emotional processing and the left amygdala (e.g., Sato, Yoshikawa, Kochiyama, & Matsumura, 2004).

Activation of the left ventromedial prefrontal (medial orbitofrontal) cortex during deceiving the interrogator might be associated with processes of social cognition such as emotional regulation, because in the DT and DL tasks, subjects had to regulate their emotional reactions to conceal their deceptive behavior, despite their higher anxiety. A recent neuroimaging study on voluntary emotion suppression suggested that the medial orbitofrontal cortex is associated with top-down regulation of peripheral physiological responses related to emotional experiences (Ohira et al., 2006). From the neuropsychological perspective, damage to the ventromedial sector of the prefrontal cortex has been believed to cause socially inappropriate behaviors (Damasio, Grabowski, Frank, Galaburda, & Damasio, 1994). Although recent studies have emphasized the importance of the right ventromedial prefrontal cortex associated with such a higher cognitive process in men (Tranel, Damasio, Denburg, & Bechara, 2005; Bolla, Eldreth, Matochik, & Cadet, 2004; Tranel, Bechara, & Denburg, 2002), Manes et al. (2002) showed that male and female patients with left orbitofrontal lesions showed abnormally long deliberation times when performing a decision-making task. Their finding indicates that the left orbitofrontal cortex in men might contribute to some extent to such higher order cognitive operation, supporting our interpretation of the role of the left ventromedial prefrontal cortex activity during deceiving the interrogator.

Contrary to our expectation, activation of the anterior cingulate cortex was not found in the main effect of falsifying the truthful responses. Anterior cingulate activity has been reported in some previous studies of deception (Mohamed et al., 2006; Kozel et al., 2005; Lee et al., 2005; Nunez et al., 2005; Kozel, Padgett, et al., 2004; Kozel, Revell, et al., 2004; Ganis et al., 2003; Langleben et al., 2002), but not in others (Davatzikos et al., 2005; Langleben et al., 2005; Phan et al., 2005; Lee et al., 2002; Spence et al., 2001). We previously reported that activity of this region was associated only with pretending not to know and suggested a role of this region as a conflict detector during deception (Abe et al., 2006). One possible reason for the present negative finding is that the form of free selection of deceptive responses in the tasks used in the present study might diminish the amount of cognitive conflict contingent

upon the competition between true and deceptive responses, although this interpretation should be directly investigated in future studies.

Other than our hypothesized regions, the results of the present study showed activations of the left precuneus (BA 7; in the main effect of lie), right anterior temporal cortices (BA 20 and BA 38; in the main effect of dishonest), and bilateral cerebellum (in both of the main effects) during deception. One possible role of the left precuneus for the process of making deceptive responses might be related to the increased cognitive demand of successful long-term memory retrieval (Cavanna & Trimble, 2006), as discussed earlier in relation to the activation of the right anterior prefrontal cortex. In support of this view, an increased blood flow in the left precuneus, together with a predominantly right-lateralized prefrontal activity, was reported in a previous PET study for the recognition of meaningful sentences (Tulving et al., 1994). The activity of the right anterolateral temporal cortices might reflect the affective aspect of deceiving the interrogator, because these regions were located within the basolateral circuit linked closely to emotional processing (Nauta, 1962). In line with this idea, the activity of the right temporal pole was shown to be associated with facial expressions (Blair, Morris, Frith, Perrett, & Dolan, 1999) and recall of affect-laden autobiographical materials (Fink et al., 1996).

The significant activations of the cerebellum were detected in three regions: one in the main effect of lie (left cerebellum) and the other two in the main effect of dishonest (bilateral cerebellum). Increased activities of the cerebellum during deception have been also reported by some previous fMRI investigations (Kozel, Revell, et al., 2004; Ganis et al., 2003). Although the cerebellum has been traditionally thought to play a role in regulating the rate, range, and force of movement (Holmes, 1939), this region might have a role for cognitive aspects associated with deception. For instance, recent studies of neuropsychological assessments of brain-damaged patients (Ravizza et al., 2006) and fMRI-guided transcranial magnetic stimulation (Desmond, Chen, & Shieh, 2005) have shown that the cerebrotocerebellar circuit was involved in verbal working memory. In addition, there was evidence for cerebellar abnormalities in emotional disorders, indicating a possible role of cerebellum for emotional regulation (Schmahmann, 2004). Considering the intimate connection between the cerebellum and the limbic system and the provided evidence for the association between cerebellum and cognitive functions (Schutter & van Honk, 2005), the cerebellar activity during deception might be possible consequences.

A limitation of the present study is the lack of correlation between brain activity and peripheral physiological responses such as skin conductance responses. Simultaneous recordings of activities derived from the central and peripheral nervous systems might further help us to dissociate regions related to somewhat different

processes associated with deception (e.g., the ventromedial prefrontal cortex and the amygdala observed in the present study). Loss-of-function studies clarifying the essential regions for a specific cognitive function, such as neuropsychological assessments of focal brain-damaged patients or application of repetitive transcranial magnetic stimulation to normal subjects, would also be beneficial. Combined studies using these methods might enable us to elucidate further the neural circuitry for human deceptive behavior.

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