



Evaluating the roles of the inferior frontal gyrus and superior parietal lobule in deductive reasoning: An rTMS study

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ABSTRACT

This study used off-line repetitive transcranial magnetic stimulation (rTMS) to examine the roles of the superior parietal lobule (SPL) and inferior frontal gyrus (IFG) in a deductive reasoning task. Subjects performed a categorical syllogistic reasoning task involving congruent, incongruent, and abstract trials. Twenty four subjects received magnetic stimulation to the SPL region prior to the task. In the other 24 subjects, TMS was administered to the IFG region before the task. Stimulation lasted for 10 min, with an inter-pulse frequency of 1 Hz. We found that bilateral SPL (Brodmann area (BA) 7) stimulation disrupted performance on abstract and incongruent reasoning. Left IFG (BA 45) stimulation impaired congruent reasoning performance while paradoxically facilitating incongruent reasoning performance. This resulted in the elimination of the belief-bias. In contrast, right IFG stimulation only impaired incongruent reasoning performance, thus enhancing the belief-bias effect. These findings are largely consistent with the dual-process theory of reasoning, which proposes the existence of two different human reasoning systems: a belief-based heuristic system; and a logic-based analytic system. The present findings suggest that the left language-related IFG (BA 45) may correspond to the heuristic system, while bilateral SPL may underlie the analytic system. The right IFG may play a role in blocking the belief-based heuristic system for solving incongruent reasoning trials. This study could offer an insight about functional roles of distributed brain systems in human deductive reasoning by utilizing the rTMS approach.

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1. Introduction

Deductive reasoning is the process of drawing valid conclusions from a given set of premises. Many theories have described the neuro-cognitive processes of human deductive reasoning. Among these, the mental model theory proposes that cognitive processes of constructing and manipulating spatially organized mental models are essential for deductive reasoning (Johnson-Laird, 1994, 2001, 2010). This predicts that the neural substrates of spatial processing (e.g., parietal cortex) are critical for human reasoning processes. Other theories have emphasized the role of language processing in deductive reasoning (e.g., Polk and Newell, 1995), predicting that the neural mechanisms of linguistic processing (e.g., left frontotemporal cortex) underwrite human reasoning processes.

Goel et al. (2000) demonstrated that the presence or absence of content words in the argument is an important factor in determining which brain mechanism is engaged. They found that the parietal lobes, including the superior parietal lobules (SPLs), were activated

bilaterally during abstract reasoning trials where semantic content was lacking (e.g., “All P are B”), consistent with the mental model theory (but see Prado et al., 2010; Reverberi et al., 2010, as studies showing the absence of SPL activation for abstract reasoning). In contrast, language-related brain regions, such as left-lateralized inferior frontal gyrus (IFG) and superior temporal lobe, were activated for contentful materials (e.g., “All dogs are mammals”), although the left IFG was also activated by abstract reasoning (Monti et al., 2007, 2009; Reverberi et al., 2007, 2010).

In addition, recent studies of the belief-bias effect have indicated that the neural correlates of content reasoning vary depending on the consistency between logical validity and belief in the conclusion (De Neys et al., 2008; Goel and Dolan, 2003; Tsujii and Watanabe, 2009, 2010). The belief-bias effect refers to the tendency for subjects to be erroneously biased when logical conclusions are incongruent with beliefs about the world (Evans, 2003). Thus, the belief-bias of semantic processing facilitates logical responses on congruent trials where the logical conclusion is consistent with beliefs about the world (valid-believable, invalid-unbelievable), while inhibiting logically correct responses on incongruent trials (valid-unbelievable, invalid-believable). Recent papers have suggested that activity in the right IFG is associated with incongruent reasoning performance, while left IFG

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activity (Brodmann area (BA) 45) is associated with congruent reasoning performance (De Neys et al., 2008; Goel and Dolan, 2003; Tsujii and Watanabe, 2009, 2010; Tsujii et al., 2010a, 2010b).

Relevant to these neuroimaging findings, the dual-process theory of reasoning proposes that human reasoning could be accomplished by flexible interactions of two different systems (Evans, 2008; Goel, 2007). The first system, often called the heuristic system, relies on prior knowledge and belief. The second, or analytic, system engages in reasoning according to logical standards. The default heuristic system is assumed to operate rapidly and automatically, while the analytic system is believed to be slow and highly demanding of computational resources (De Neys, 2006a, 2006b; Tsujii and Watanabe, 2009, 2010). The analytic system is necessary for solving abstract and incongruent reasoning, while the heuristic system is sufficient for performing congruent reasoning.

According to this dual process theory, the left frontotemporal pathway (e.g., left IFG) corresponds to the belief-based heuristic system, whereas the bilateral parietal pathway (e.g., SPL) corresponds to the logic-based analytic system (Goel, 2007). Right IFG may play a functional role as a switching mechanism to inhibit the default heuristic system and thus enable analytic system activity (Tsujii and Watanabe, 2009, 2010). These considerations, although interesting, have only been supported by neuroimaging studies, which can only examine correlations between cortical areas and a type of behavior. The aim of the present study was to examine the roles of the SPL and IFG in a deductive reasoning task using repetitive transcranial magnetic stimulation (rTMS) to establish causal relationships between brain and behavior more directly.

Another recent study examined neural correlates of the deductive reasoning process using an off-line rTMS method (Tsujii et al., 2010a). They adopted an approach in which low-frequency rTMS is delivered to a specific brain area over several minutes to disrupt normal functioning transiently after stimulation (for a review, see Robertson et al., 2003). Tsujii et al. (2010a) examined the role of the IFG in belief-bias reasoning using this temporal lesion approach and found that subjects in whom the right IFG was impaired by rTMS could not inhibit irrelevant semantic processing in incongruent reasoning, resulting in an enhanced belief-bias effect. In contrast, left IFG stimulation significantly impaired congruent reasoning performance while paradoxically facilitating incongruent reasoning performance. Left IFG stimulation removed interference from irrelevant semantic processing, resulting in elimination of the belief-bias effect.

Two shortcomings of this pioneering research must be mentioned: they only examined the region around the IFG; and they did not examine abstract reasoning where semantic-content was lacking. The present study examined the roles of the SPL and IFG in a deductive reasoning task using the same off-line rTMS approach. The task

included congruent, incongruent, and abstract reasoning trials (Fig. 1), and our study addressed how these three types of reasoning performance were affected by magnetic stimulation of the SPL and IFG.

2. Methods

2.1. Subjects

Twenty four subjects were assigned to the SPL group (13 women, 11 men; 23 were right-handed) and the other 24 were assigned to the IFG group (12 women, 12 men; 22 were right-handed). Mean age was 21.33 ± 1.88 years for the SPL group and 21.54 ± 1.93 years for the IFG group. None had received any formal training in logic. The study was conducted in accordance with the principles of the Declaration of Helsinki and the guidelines from the International Workshop on the Safety of Repetitive Transcranial Magnetic Stimulation (Wassermann, 1998), and the protocol was approved by the Ethics Committee of Keio University. Written informed consent was obtained from all subjects prior to enrolment in the study.

2.2. Materials

We prepared 144 contentful and 72 no-content abstract syllogisms (Fig. 1). Contentful syllogisms included sentences like “All pigeons are birds”, while no-content abstract sentences were of the form “All S are Z”. For contentful syllogisms, a combination of logical validity and believability yielded two types of trials: 72 congruent (36 valid-believable, 36 invalid-unbelievable) and 72 incongruent (36 valid-unbelievable, 36 invalid-believable). The believability of the conclusion was rated by five independent subjects prior to the experiment using a seven-point questionnaire (1 = “completely unbelievable” to 7 = “completely believable”). Mean believability scores were 6.54 for believable syllogisms ($SD = 0.39$; $range = 5.4-7.0$) and 1.71 for unbelievable syllogisms ($SD = 0.55$; $range = 1.0-2.8$). For the no-content abstract syllogisms, half of the arguments were valid.

We presented 12 types of valid arguments (AOO-2, AII-3, EAE-1, EAE-2, AEE-2, AEE-4, IAI-3, IAI-4, OAO-3, EIO-4, AAA-1 [presented twice]) and 12 types of invalid arguments (AEE-1, AAA-3, AII-2, EAE-4, AAE-2, EEE-2, EEA-4, AOO-3, OAO-1, IIA-4, EII-3, EIE-1) for each reasoning condition (congruent, incongruent, and abstract). The important point is that the argument types (logical forms) did not differ among these three types of reasoning condition.

2.3. Procedures

Individual subjects visited our laboratory 12 times: 4 times for left hemisphere stimulation; 4 times for right hemisphere stimulation;

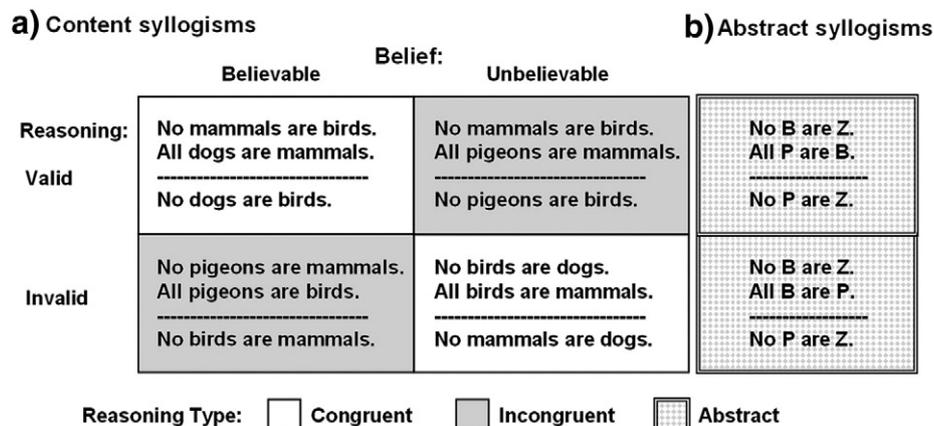


Fig. 1. Experimental design showing examples of the six types of reasoning trial. a) Contentful syllogisms were further classified as congruent or incongruent syllogisms by the combination of logical validity and believability of the conclusion. b) Abstract syllogisms.

and another 4 times for control stimulation. Subjects were randomly assigned to either SPL or IFG stimulation groups, and the control stimulation site was Pz or Fz for each group, respectively. The order of stimulation sites was randomly determined.

Immediately after 10 min of magnetic stimulation, subjects were asked to perform a categorical syllogistic reasoning task. The reasoning task was run using a personal computer. For each visit, there were 18 reasoning trials (6 congruent, 6 incongruent, and 6 abstract syllogisms); these trials were drawn from 72 reasoning trials for each stimulation condition. The three types of syllogisms were presented in randomly intermixed order. A 20-s time limit was set for each trial, signaled by an asterisk (*) for 500 ms at the beginning. The total task time was thus 6 min for each visit, within the time range during which low-frequency rTMS inhibits regional brain activity (Robertson et al., 2003). We simultaneously presented all components of the syllogisms (major premise, minor premise, and conclusion). Subjects were asked to respond to the validity of each syllogism by mouse click: left click if the given syllogism was valid and right if it was invalid. Subjects were able to change responses as many times as needed within the time range of each trial (20 s). In addition, they were not instructed to respond as fast as possible. Instructions emphasized that the premises should be assumed to be true and that a conclusion should be accepted only if following logically from the premises.

2.4. Magnetic stimulation

Prior to the rTMS experiment, a whole-brain anatomical image was obtained from each participant in a 3-T magnetic resonance scanner (Trio-Tim; Siemens AG, Erlangen, Germany). The T1-weighted data set was acquired with the help of a magnetization-prepared rapid acquisition gradient echo sequence (208 slices, matrix size = 256 × 256, thickness = 1 mm).

The location of coil placement was determined using an MRI-image-guided stereotactic system (Brainsight; Rouge Research, Montreal, Canada) and the individual high-resolution image from T1-weighted MRI of each participant. This system displays the position of the TMS coil on the three-dimensional (3D) magnetic resonance image with 2-mm precision. Half of the subjects received stimulations to each of the left SPL, right SPL and a control site, Pz (International 10–20 system). For SPL stimulation (BA 7), we stimulated the area just above the intraparietal sulcus (Fig. 2).

The remaining subjects received stimulations to each of the left IFG, right IFG, and Fz. The IFG consists of three areas: pars opercularis; pars triangularis (Ptr); and pars orbitalis (POr). These correspond roughly to BA 44, 45, and 47, respectively. We selected Ptr (BA 45) as the stimulation site in the present study. More specifically, we stimulated the area just superior to the horizontal ramus of the Sylvian fissure (Fig. 3), meaning that we stimulated the most ventral parts of Ptr (BA 45), near the borderline of POr (BA47). Fz was used for a midline control site.

A MagStim Rapid magnetic stimulator (MRS1000/30; Magstim, Whitland, UK) connected with a figure-eight coil with a diameter of 70 mm was used to deliver rTMS trains at an intensity of 100% of resting motor threshold. The magnetic stimulus had a biphasic waveform with a pulse width of approximately 300 μs. Resting motor threshold was determined as the minimum stimulus intensity able to elicit a visible muscle twitch in the contralateral hand in 50% of a sequence of 10 consecutive single-pulse stimulations. We determined the resting motor threshold at the first visit of each subject. Average motor thresholds were 611.3 mT ($SD=93.2$) for the SPL group and 609.6 mT ($SD=94.0$) for the IFG group. No significant differences in resting motor thresholds were seen between subject groups ($t(46)=0.06$, $p=0.95$, $\eta^2=.00$). Stimulation lasted for 10 min, with an inter-pulse frequency of 1 Hz. This off-line method has been shown to transiently attenuate activity of the underlying cortex (for review, see Robertson et al., 2003).

2.5. Data analysis

Accuracy scores were calculated by dividing the number of trials in which subjects correctly judged validity of arguments by the total number of trials. Scores were statistically tested using three-way analysis of variance (ANOVA) using one between-subject factor of location group (SPL, IFG) and two within-subject factors of reasoning type (congruent, incongruent, and abstract) and hemisphere (right hemisphere, left hemisphere, and control sites [Fz for the frontal group and Pz for the parietal group]). As the second-order interaction was significant ($F(4184)=8.20$, $p<.01$, $\eta_p^2=.15$), separate 2-way (reasoning type × hemisphere) ANOVAs were performed for each location group. In addition, separate 2-way ANOVAs (reasoning type × location group) were performed for each hemisphere condition (right hemisphere, left hemisphere, and control sites) for between-subject comparisons. The

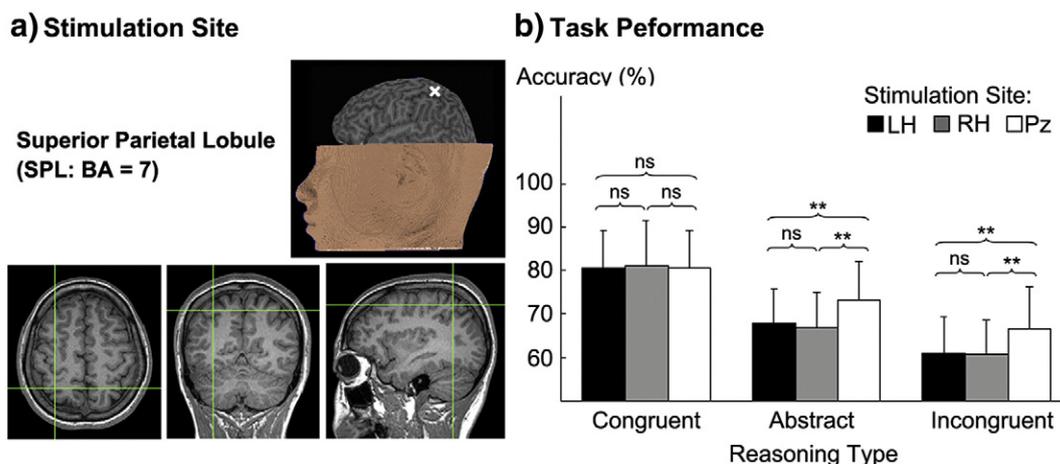


Fig. 2. a) Site of magnetic stimulation of the superior parietal lobule (SPL: BA = 7). The upper image shows the 3D model created using a frameless stereotactic system. The lower photographs show axial, coronal, and transverse MRI, respectively. b) Accuracy as a function of stimulation condition and reasoning type. Significant comparisons are shown; * $p<0.05$; ** $p<.01$.

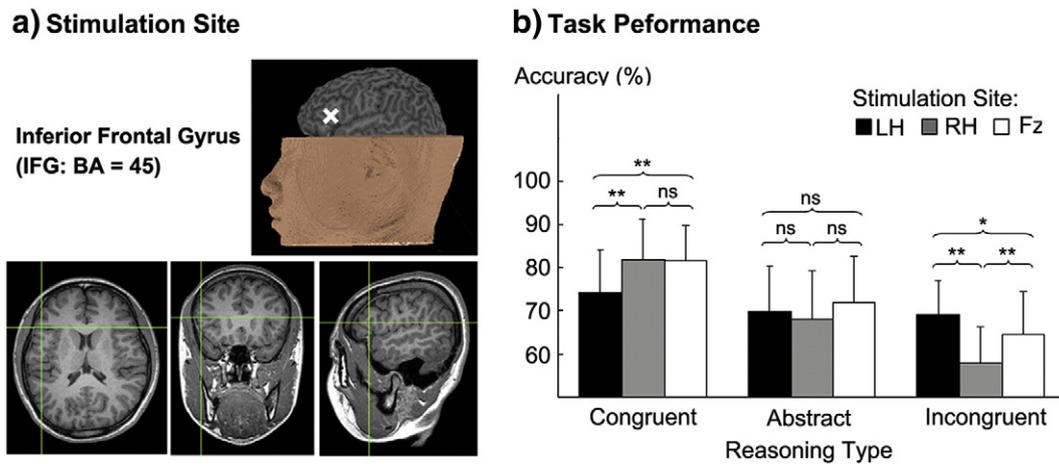


Fig. 3. a) Locus of magnetic stimulation for the inferior frontal gyrus (IFG: BA = 45). The upper image shows the 3D model created using a frameless stereotactic system. The lower photographs show axial, coronal, and transverse MRI, respectively. b) Accuracy as a function of stimulation condition and reasoning type. Significant comparisons are shown; * $p < .05$; ** $p < .01$.

effect size (η^2 for t -test or η_p^2 for ANOVA) was also calculated for the sake of future meta-analyses (Field, 2005; Kline, 2004).

3. Results

3.1. SPL

Fig. 2 summarizes accuracy scores from congruent, incongruent, and abstract reasoning trials after the SPL regions were stimulated. Two-way ANOVA revealed a significant hemisphere \times reasoning type interaction ($F(4,92) = 2.51, p < .05, \eta_p^2 = .10$), suggesting that significant hemisphere effects were observed for abstract trials ($F(2,138) = 6.62, p < .01, \eta_p^2 = .10$), and for incongruent trials ($F(2,138) = 6.18, p < .01, \eta_p^2 = .09$), but not for congruent trials ($F(2,138) = .05, p = .95, \eta_p^2 = .00$).

For abstract reasoning trials, paired comparison analysis (Ryan's method) showed that subjects performed significantly better after Pz stimulation ($M = .73, SD = .09$) relative to both left SPL stimulation ($M = .68, SD = .08, t(138) = 2.82, p < .01, \eta^2 = .05$) and right SPL stimulation ($M = .67, SD = .08, t(138) = 3.34, p < .01, \eta^2 = .07$).

Similar results were found for incongruent reasoning trials. Again, paired comparison analysis showed that subjects performed significantly better after Pz stimulation ($M = .67, SD = .09$) compared with both left SPL stimulation ($M = .61, SD = .08, t(138) = 3.01, p < .01, \eta^2 = .06$) and right SPL stimulation ($M = .61, SD = .08, t(138) = 3.08, p < .01, \eta^2 = .06$). In either hemisphere, SPL stimulation significantly impaired performance in abstract and incongruent reasoning trials, but no significant effect of SPL stimulation was seen for congruent reasoning trials. No significant hemispheric differences were identified for the effects of SPL stimulation.

3.2. IFG

Fig. 3 summarizes accuracy scores from congruent, incongruent, and abstract reasoning trials after the IFG regions were stimulated. Two-way ANOVA revealed a significant hemisphere \times reasoning type interaction ($F(4,92) = 14.06, p < .01, \eta_p^2 = .38$), suggesting that significant hemisphere effects were observed for congruent trials ($F(2,138) = 8.96, p < .01, \eta_p^2 = .13$) and incongruent trials ($F(2,138) = 15.70, \eta_p^2 = .23$), but not for abstract trials ($F(2,138) = 1.94, p = .15, \eta_p^2 = .03$).

For congruent reasoning trials, paired comparison analysis showed that reasoning performance was significantly impaired by left IFG stimulation ($M = .74, SD = .10$) relative to right IFG stimulation ($M = .82, SD = .10, t(138) = 3.72, p < .01, \eta^2 = .09$) and relative to Fz stimulation ($M = .81, SD = .08, t(138) = 3.61, p < .01, \eta^2 = .09$). No

significant differences were observed between right IFG stimulation and Fz stimulation ($t(138) = .10, p = .92, \eta^2 = .00$). That is, only stimulation of the left IFG impaired congruent reasoning performance. In contrast, paired comparison analysis showed that right IFG stimulation significantly impaired performance on incongruent reasoning trials ($M = .58, SD = .09$) compared with Fz stimulation ($M = .64, SD = .09, t(138) = 3.28, p < .01, \eta^2 = .07$), while left IFG stimulation ($M = .69, SD = .08$) significantly improved reasoning performance compared with Fz stimulation ($M = .64, SD = .09, t(138) = 2.30, p < .05, \eta^2 = .04$).

The significant hemisphere \times reasoning type interaction also indicated that significant reasoning type effects were observed in both right IFG stimulation ($F(2,138) = 48.57, p < .01, \eta_p^2 = .70$) and Fz stimulation ($F(2,138) = 24.71, p < .01, \eta_p^2 = .36$), but not in left IFG stimulation ($F(2,138) = 2.60, p = .08, \eta_p^2 = .04$). With right IFG stimulation, subjects performed significantly better for congruent reasoning trials ($M = .82, SD = .10$) than for abstract reasoning trials ($M = .68, SD = .11, t(138) = 5.56, p < .01, \eta^2 = .18$), and in turn for abstract reasoning trials than for incongruent reasoning trials ($M = .58, SD = .09, t(138) = 4.26, p < .01, \eta^2 = .12$). A similar pattern was also observed in Fz stimulation. Paired comparison analysis showed that subjects performed significantly better for congruent reasoning trials ($M = .81, SD = .08$) than for abstract reasoning trials ($M = .72, SD = .11, t(138) = 3.85, p < .01, \eta^2 = .10$), and in turn for abstract reasoning trials than for incongruent reasoning trials ($M = .64, SD = .10, t(138) = 3.17, p < .01, \eta^2 = .07$).

3.3. Between-subject comparisons

For between-subject comparison, we conducted 2 (location group: SPL vs. IFG) \times 3 (reasoning type: congruent, incongruent, and abstract) ANOVAs for each hemisphere condition (right hemisphere, left hemisphere, and control [midline] sites). No significant main effects of location group were seen for the right hemisphere ($F(1,46) = 0.03, p = .86, \eta_p^2 = .00$), left hemisphere ($F(1,46) = 0.64, p = .43, \eta_p^2 = .01$) or control site ($F(1,46) = 0.18, p = .67, \eta_p^2 = .00$). The location group \times reasoning type interaction was only significant when the left hemisphere was stimulated ($F(2,92) = 8.64, p < .01, \eta_p^2 = .16$), suggesting that left IFG stimulation ($M = .74, SD = .10$) impaired congruent reasoning performance significantly more than left SPL stimulation ($M = .81, SD = .09, F(1,138) = 6.05, p < .05$), whereas left IFG stimulation ($M = .69, SD = .08$) impaired incongruent reasoning performance significantly less than left SPL stimulation ($M = .61, SD = .08, F(1,138) = 9.83, p < .01$). No significant difference in abstract reasoning

performance was apparent between left SPL ($M = .68$, $SD = .08$) and left IFG stimulation ($M = .70$, $SD = .11$, $F(1138) = 0.67$, $p = .41$). The location group \times reasoning type interaction was not significant for the right hemisphere ($F(2,92) = 0.95$, $p = .39$, $\eta_p^2 = .02$) or control site stimulation ($F(2,92) = 0.51$, $p = .60$, $\eta_p^2 = .01$).

4. Discussion

The present study examined the role of the SPL and IFG in a deductive reasoning task (Robertson et al., 2003). The rTMS parameters used here are known to transiently disrupt the activity of targeted brain regions in a variety of tasks (Hilgetag et al., 2001; Kosslyn et al., 1999; Miller et al., 2008; Robertson et al., 2003). Subjects performed a categorical syllogistic reasoning task which included congruent, incongruent, and abstract trials. Here we discuss how these three types of reasoning performance were affected by rTMS in the SPL and IFG regions, and how the results support the dual-process theory of reasoning, which proposes the existence of a belief-based heuristic system and a logic-based analytic system as interacting reasoning systems.

4.1. Bilateral SPL and spatial processing

We found that SPL stimulation significantly impaired performance in abstract and incongruent reasoning trials without affecting congruent reasoning performance. No hemispheric difference was observed for SPL stimulation. These findings suggest that the activity of bilateral SPLs was critical when semantic content was absent or conflicted with the logical validity.

The present findings could support the predominant theory of reasoning, which states that spatial processing plays an important role in abstract reasoning (Goel, 2007; Johnson-Laird, 1994, 2001, 2010). For example, Johnson-Laird et al. have proposed the mental model theory, which states that reasoning is a cognitive process in which spatially organized mental models are used to draw a conclusion from premises (Johnson-Laird, 1994, 2001, 2010; Knauff et al., 2002, 2003; Knauff and Johnson-Laird, 2002; Knauff and May, 2006). In this theory, mental models are a form of representation that can be spatial but more abstract. Phenomenological reports in the reasoning literature often have suggested that subjects may solve abstract syllogisms through the use of mental images of Venn diagrams and Euler circles (Goel et al., 2000; Goel and Dolan, 2001). SPL is associated with spatial processing based on evidence from functional MRI (fMRI) studies (Takahama et al., 2010; Thakral and Slotnick, 2009; van der Ham et al., 2009), neurological patients (Ferber and Danckert, 2006; Shinoura et al., 2009) and rTMS studies (Hamidi et al., 2008, 2009; Sack et al., 2002). Stimulation of the SPL may thus have impaired abstract and incongruent reasoning by disrupting spatial processing. In contrast, congruent reasoning performance where semantic-based heuristics are sufficient to solve the problem was unimpaired.

Two issues must be taken into account before making strong and general claims about the role of the SPL in deductive reasoning. First, only verbal syllogistic reasoning tasks could support the framework that the SPL mediates analytic system while the left IFG mediates heuristic system. For example, Stavy et al. (2006) used a spatial reasoning task to demonstrate that the SPL is associated with intuitive-based heuristic processes, rather than analytic logical thinking. This finding suggests that the role of SPL can vary depending on the reasoning task and that some caution is warranted before generalizing the basic claims of the dual-process theory.

Second, an alternative possibility is that the SPL effect is not due to the inhibition of “core” deduction processes, but is instead due to the non-deductive processes, such as attention and working memory (Monti et al., 2007, 2009; Reverberi et al., 2010). Indeed, Monti et al. (2007, 2009) classified brain regions of the formal (or analytic)

reasoning system into “core” areas (BA 8/10) and “support” areas (BA 6, 7, 8, 40, and 47), were associated with increased cognitive load, working memory, and executive processes. According to that theory, stimulation of the SPL (BA 7) impaired abstract and incongruent reasoning trials compared with congruent reasoning trials because the former were more attention-demanding processes than the latter. The present findings cannot exclude this alternative possibility. Although we do not claim that the analytic system is independent of attention and working memory, this is quite an important problem. Future work should clarify this problem by targeting the core reasoning area (BA 8/10).

4.2. Left IFG and semantic processing

Stimulation of the language-related left IFG (BA 45) impaired congruent reasoning performance while paradoxically facilitating incongruent reasoning performance. As a result, the belief-bias effect was eliminated. In addition, left IFG (BA 45) stimulation did not affect abstract reasoning performance. The pattern of results was consistent with a previous rTMS study (Tsujii et al., 2010b) and fMRI studies (Goel et al., 2000, 2009; Goel and Dolan, 2003). The left IFG is generally thought to be associated with verbal or semantic processing in a wide variety of tasks, including semantic decision tasks (Devlin et al., 2003; Newman and Joanisse, 2011; Olichney et al., 2010), verbal fluency tasks (Costafreda et al., 2006; Tsujii et al., 2009), and sentence comprehension tasks (Thompson et al., 2010; Zhu et al., 2009). For example, Devlin et al. (2003) delivered magnetic stimulation to PTR (BA45) in the left IFG, resulting in significantly delayed responses in a semantic decision task.

According to the dual-process theory of reasoning, individuals can solve congruent trials correctly by relying on either logic-based or belief-based reasoning. If the belief-based route is blocked, the individual will need to rely on the logical route. It is well established that logic-based analytic reasoning is more demanding than belief-based heuristics (De Neys, 2006a, 2006b; Tsujii and Watanabe, 2009, 2010). For this reason, left IFG stimulation impaired reasoning performance of congruent trials. On the other hand, the belief-based route interferes with logical reasoning for incongruent trials. Blocking the irrelevant belief-based route by stimulating the left IFG thus paradoxically improves reasoning performance for incongruent trials by eliminating the belief-bias effect.

Of note is the fact that our claims about the role of left IFG only cover the language-related areas (BA 45). Recent fMRI studies have found that the rostralateral prefrontal cortex (BA 10/47) is activated by abstract reasoning (Monti et al., 2007, 2009; Prado et al., 2010; Reverberi et al., 2010). These findings suggest that the left IFG is not simply associated with the belief-based heuristic system. Although the posterior IFG (BA 44/45) is strongly associated with language processing, more anterior parts of the IFG (BA 10/47) are associated with abstract reasoning process. Our findings do not seem incompatible with the proposed role of BA 10/47 in deductive reasoning (Monti et al., 2007, 2009). Future works are expected to clarify the functional roles of the posterior IFG (BA 44/45) and anterior IFG (BA 10/47).

4.3. Right IFG and inhibitory processing

Right IFG stimulation significantly impaired reasoning performance of incongruent but not congruent trials, enhancing the belief-bias effect. This is consistent with the findings of previous studies using fMRI and functional near-infrared spectroscopy that implicated right IFG activity in incongruent reasoning. For example, Goel and Dolan (2003) found that right IFG activity was enhanced when subjects responded correctly to incongruent reasoning trials. Moreover, recent fNIRS studies have found that subjects with enhanced right IFG activity performed better in incongruent reasoning (Tsujii and Watanabe, 2009, 2010; Tsujii et al., 2009).

Right IFG activity is generally known to play a central role in inhibitory function (Aron et al., 2004a, 2004b). Response inhibition has been found to be associated with right IFG activity in several tasks, including the go/no-go task (Chikazoe et al., 2007; Berkman et al., 2009) and the stop-signal task (Aron and Poldrack, 2006; Boecker et al., 2007). Furthermore, right IFG activity was enhanced when subjects changed from one task to another (task-set switching) (Aron et al., 2004a, 2004b; Xue et al., 2008). In the belief-bias reasoning paradigm, relevant semantic information processing should disturb reasoning performance in incongruent trials, while facilitating performance in congruent trials. Thus, to resolve conflicts in reasoning, subjects must inhibit the semantic processing associated with heuristic beliefs. When rTMS impaired the inhibitory function of the right IFG, subjects could not respond correctly for incongruent trials, enhancing the belief-bias response and indicating that inhibitory activity by the right IFG was necessary for incongruent reasoning.

De Neys and Franssens (2009) recently investigated the nature of the inhibition process in belief-bias reasoning. In their experiments, subjects performed a lexical decision task after solving the deductive reasoning task which involved congruent and incongruent trials. They found that incongruent reasoning delayed lexical decisions regarding the target word that were relevant to the cued heuristic beliefs. Interestingly, no significant difference was apparent between congruent and incongruent reasoning trials for unrelated words. That is, the accessibility of unrelated words was unaffected. This suggests that the inhibition process is focused in nature and is specifically targeted at cued beliefs, not at semantic processing in general.

In addition, it should be noted that right IFG stimulation did not significantly impair abstract reasoning performance compared with left IFG and control (Fz) stimulation conditions (Fig. 3). Right IFG stimulation impaired only incongruent trials in the present findings. In contrast, SPL stimulation significantly impaired both abstract and incongruent reasoning performance (Fig. 2). These findings suggest that the SPL, not the right IFG, is the neural locus of the analytic reasoning system. The right IFG may play a role in blocking the belief-based heuristic system (left IFG) in solving incongruent reasoning trials. On the other hand, individuals need not actively inhibit the heuristic processing on abstract trials, so right IFG stimulation did not significantly affect abstract reasoning performance.

4.4. Conclusions

This study examined the roles of the SPL and IFG in a deductive reasoning task using an off-line rTMS method. The findings are largely consistent with the dual-process theory of reasoning, which proposes the existence of two different reasoning systems in humans: a belief-based heuristic system; and a logic-based analytic system. In the present study, the left IFG appears to correspond to the heuristic system, while bilateral SPLs are part of the analytic system. The right IFG may play a role in blocking the belief-based heuristic system (left IFG) in solving incongruent reasoning trials. The present study could offer an insight about functional roles of distributed brain systems in human deductive reasoning by utilizing the rTMS approach.

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