



Uncertain relational reasoning in the parietal cortex

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ABSTRACT

The psychology of reasoning is currently transitioning from the study of deductive inferences under certainty to inferences that have degrees of uncertainty in both their premises and conclusions; however, only a few studies have explored the cortical basis of uncertain reasoning. Using transcranial magnetic stimulation (TMS), we show that areas in the right superior parietal lobe (rSPL) are necessary for solving spatial relational reasoning problems under conditions of uncertainty. Twenty-four participants had to decide whether a single presented order of objects agreed with a given set of indeterminate premises that could be interpreted in more than one way. During the presentation of the order, 10-Hz TMS was applied over the rSPL or a sham control site. Right SPL TMS during the inference phase disrupted performance in uncertain relational reasoning. Moreover, we found differences in the error rates between preferred mental models, alternative models, and inconsistent models. Our results suggest that different mechanisms are involved when people reason spatially and evaluate different kinds of uncertain conclusions.

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1. Introduction

Psychologists and cognitive neuroscientists have investigated human *deductive* reasoning for many years (reviewed in Goel, 2007; Knauff, 2007; Prado, Chadha, & Booth, 2011). An inference is deductively valid if the conclusion is *certainly* true, given that the premises are true. *Conditional reasoning* relies on if–then arguments, *categorical syllogisms* on quantifiers (such as all, some, or none), and *relational reasoning* on spatial, temporal, or other types of relational expressions. Psychologists found that some of these deductive inferences are simple for most people but the same people commit many logical errors in other reasoning tasks. People's logical errors are not random but instead show many systematic deviations from logical norms (e.g., Evans, 1989; Manktelow, 1999). Different cognitive theories explain these deviations from classical formal logic by means of mental inference rules, mental models, or probabilistic theories of reasoning (Johnson-Laird, 2006; Oaksford & Chater, 2007; Rips, 1994; Van der Henst, 2002).

Cognitive neuroscientists explored the neural basis of *deductive* reasoning primarily via functional brain-imaging techniques and

patient studies; they identified a complex fronto-temporo-parietal network as the basis of logical reasoning (Goel, 2007; Knauff, 2009a, 2009b; Prado et al., 2011). The findings were again not random. They show that bilateral temporal and parietal brain areas are involved in conditional and syllogistic reasoning, whereas areas in the right parietal cortex are involved in relational inferences. Prefrontal brain areas are involved in executive functions and conflict resolution processes during reasoning (Goel et al., 2007; Knauff, 2009). Moreover, a lateralized frontal–temporal system processes inferences with familiar content, whereas abstract logical inferences are processed in the right parietal cortical areas (Goel & Dolan, 2003).

Recent progress in these fields has been significant, but criticism of the deductive paradigm has increased. A primary criticism is that deductive reasoning that focuses on truth-preserving inferences does not resemble how people often reason in their everyday lives. Reasoning in daily life is often *uncertain*. While reasoning we often do not know that a conclusion necessarily follows from what we know but rather that it is more or less likely, plausible, or believable. Psychologists have investigated such uncertain inferences but to a lesser extent than certain deductive reasoning (Johnson-Laird, 2006; Johnson-Laird, Girotto, & Legrenzi, 2004; Oaksford & Chater, 2007). Only a few cognitive neuroscientists have investigated the neural basis of uncertainty in reasoning (e.g., Goel, Stollstorff, Nakic, Knutson, & Grafman, 2009;

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Waechter, Goel, Raymont, Kruger, & Grafman, 2013); we describe these studies below.

Here, we focus on *uncertain relational reasoning*. From the following premises, can you determine the order of the pear and the mango with certainty?

The apple is to the left of the lemon.
The lemon is to the left of the pear.
The mango is to the left of the orange.
The lemon is to the left of the mango.

No, you cannot give a certain answer to this question because the premises are *indeterminate*. No matter what arrangement you imagine, you can always think of another possibility that is also consistent with the premises. In the example, two arrangements agree with the premises:

| | | | | | |
|-----|-------|-------|-------|--------|--------|
| (1) | apple | lemon | pear | mango | orange |
| (2) | apple | lemon | mango | orange | pear |

Each line denotes a possibility in which the premises hold true. However, it is impossible to know for certain which of the arrangements might be the real arrangement. Therefore, for such uncertain relational descriptions no deductively valid inference is possible (except that nothing follows for the arrangement between the pear and the mango). Whenever you choose one of the possibilities, your decision has a certain *degree of uncertainty*.

Previous cognitive experiments have shown that people deal with such uncertain spatial reasoning problems by considering just one of the possibilities and ignoring others. For instance, the majority of people would choose, for the two alternatives presented above, the order in the first line (1) and act as if possibility (2) does not exist (Jahn, Knauff, & Johnson-Laird, 2007; Rauh et al., 2005).

The *theory of preferred mental models* (PMMs) explains such preferences (Knauff, 2013; Ragni & Knauff, 2013). In this theory the preferred possibility (1) is the *preferred mental model* (PMM) and the other possibility (2) is the *alternative mental model* (AMM; please refer to Table 1). The study presented below had two goals: to explore the causal role of the right superior parietal cortex in reasoning in light of uncertain relational premises, and to determine whether these brain areas are differentially involved in the processing of PMMs (1), AMMs (2), and *inconsistent models* (IMMs) (3, 4). IMMs are orders of objects that conflict with the given premises, for example:

| | | | | | |
|-----|--------|-------|------|-------|--------|
| (3) | orange | lemon | pear | mango | apple |
| (4) | apple | mango | pear | lemon | orange |

This article begins with a summary of what is known about the cortical basis of human reasoning with relations, followed by a description of the theory of PMMs. The PMM is the mental model of uncertain premises that comes to the reasoner's mind first and guides the inference process as long as nothing contradicts it. Based on this theory, we predict that the human brain processes PMMs, AMMs, and IMMs differently. In the main body of this article, we describe the transcranial magnetic stimulation (TMS; e.g., Walsh & Pascual-Leone, 2003) experiment in which we temporarily hindered neural processing in the right superior parietal lobe (rSPL). We chose this area based on previous studies with patients and fMRI, as described below. In the discussion, we argue that PMMs

Table 1
An indeterminate problem and the three types of models.

| | | | | | |
|------------|---------------------------------|-------|-------|--------|--------|
| 1. Premise | The apple is left of the lemon | | | | |
| 2. Premise | The lemon is left of the pear | | | | |
| 3. Premise | The mango is left of the orange | | | | |
| 4. Premise | The lemon is left of the mango | | | | |
| Models | apple | lemon | pear | mango | orange |
| | apple | lemon | mango | orange | pear |
| | orange | lemon | pear | mango | apple |
| | apple | mango | pear | lemon | orange |

PMM
AMM
IMM
IMM

play an important role in uncertain spatial reasoning and that the rSPL is causally relevant to these uncertain relational inferences.

1.1. Previous findings from patient studies, fMRI, TMS, and NIRS

In the following, we summarize results from (1) patient studies on relational reasoning under certainty, (2) brain-imaging studies on reasoning under certainty, (3) patient studies on relational reasoning under uncertainty, (4) brain-imaging studies on uncertain reasoning, and (5) TMS and near-infrared spectroscopy (NIRS) studies on human reasoning.

1.1.1. Patient studies of relational reasoning under certainty

In an early study, Caramazza, Gordon, Zurif, and DeLuca (1976) presented relational statements, such as "Mike is taller than George" to patients with right or left brain hemisphere lesions. After reading the statements, the patients had to answer either a congruent ("Who is taller?") or incongruent ("Who is shorter?") question. The left-hemispheric lesion patients were more impaired in the congruent problems and, in contrast, the right-hemispheric lesion patients were more impaired in the incongruent problems. Read (1981) reported similar results with "real" inference problems consisting of two relational premises and congruent and incongruent conclusions that were deductively valid or invalid. Goel et al. (2007) studied patients with lateralized focal lesions to the right and left prefrontal cortices (PFCs) and healthy controls. In their study, the authors used transitive relations, such as "A is to B and B is to C; how is A to C?" Such inferences can be either valid or invalid and determinate or indeterminate; for instance, premises such as $A > B$ and $B > C$ are determinate and the logically valid conclusion is $A > C$, whereas the conclusion $C > A$ is inconsistent with the premises and thus deductively invalid. In contrast, indeterminate premises, such as $A > B$ and $A > C$, do not provide enough information to construct a single model, and three models are possible: $A > B > C$, $A > C > B$, or $A > (B = C)$. Goel and colleagues asked patients to determine the relationship between B and C. For these objects, no valid conclusion exists (except that nothing follows for the arrangement of B and C) because in the first model $B > C$ holds, in the second model $C > B$ holds, and in the third model $B = C$ holds. Goel and colleagues showed that patients with left PFC lesions were impaired in inferences with determinate premises (i.e., certain) and patients with right PFC lesions were impaired in inferences with indeterminate premises (i.e., uncertain). These results indicate that the right PFC is involved in the processing of uncertain information and ambiguity, a result that is supported by other studies (e.g., Koscik & Tranel, 2012; Vartanian & Goel, 2005).

1.1.2. Brain-imaging studies on relational reasoning under certainty

Goel, Gold, Kapur, and Houle (1998) and Knauff, Mulack, Kassubek, Salih, and Greenlee (2002) reported the first brain-imaging studies on relational reasoning. Goel and Dolan (2001) addressed activity in visual association areas using sentences with spatial content that was either concrete (e.g., "The apples are in the

barrel; the barrel is in the barn; therefore the apples are in the barn") or abstract (e.g., "A are in B; B is in C; therefore A is in C"). These authors reported that all the problems activated a similar bilateral occipito-parietal network regardless of whether the problems were concrete or abstract. Additional work by [Goel and Dolan \(2003\)](#) investigated conflicts between logic and beliefs and found evidence for the engagement of a left temporal lobe system during belief-based reasoning and a bilateral parietal lobe system during belief-neutral reasoning. [Prado et al. \(2011\)](#) analyzed 28 studies of deductive reasoning and showed that both the bilateral posterior parietal cortex (PPC) and the middle frontal gyrus (MFG) were activated during relational reasoning. Eighteen out of 22 fMRI studies showed lateral SPL activation during relational reasoning; the right parietal lobe was activated in at least 15 of the studies ([Ragni, Franzmeier, Wenczel, & Maier, 2014](#)).

1.1.3. Patient studies on relational reasoning under uncertainty

A patient study by [Goel et al. \(2007\)](#) found that damage to the right PFC was associated with a significant decrease in the performance of processing and resolving indeterminate (uncertain) but not determinate (certain) relations. Similarly, an overview by [Krawczyk \(2012\)](#) found significant PFC involvement in visual spatial integration and parietal cortex involvement in visual spatial representation in relational and analogical reasoning. Recently, the focus has shifted from the PFC to the PPC. A study by [Waechter et al. \(2013\)](#), for instance, compared impairments of the rostralateral PFC and the parietal cortex in relational transitive inferences containing indeterminate and inconsistent problems, and their results support the dominant role of the parietal cortex in transitive reasoning. In fact, nearly all of the PPC-impaired patients in the study had damage in BA 7 and showed an overall accuracy of about 49%; on the other hand, rostralaterally-impaired patients and normal controls showed overall accuracies on the same reasoning problems of about 67% and 70%, respectively.

1.1.4. Brain-imaging studies on relational reasoning under uncertainty

Only a few studies have investigated relational reasoning under uncertainty using brain imaging. In one of the first studies about certain and uncertain reasoning, [Goel, Makale, and Grafman \(2004\)](#) showed that contrasts between familiar and unfamiliar spatial problems led to SPL involvement. A more in-depth investigation by [Goel et al. \(2009\)](#) focused on the role of the PFC in reasoning about belief-bias cues in indeterminate problems; their findings showed that the roles of the left and right PFC in reasoning about indeterminate problems were dependent on the belief-bias cues. If these cues were given, patients used the left PFC; if the cues were absent, the patients used the right PFC. Additionally, they found that the right parietal cortex (BA 7) and the precuneus were particularly activated in the contrasts between familiar (without the unfamiliar problems) indeterminate and familiar (without the unfamiliar problems) determinate problems.

1.1.5. TMS studies on human reasoning

Our study is not the first TMS study on reasoning but is the first on relational reasoning and uncertainty, e.g., [Tsujii, Sakatani, Masuda, Akiyama, and Watanabe \(2011\)](#) used TMS to study syllogistic reasoning. The theoretical background of this study is the dual-process theory of reasoning, which postulates different cognitive and cortical systems for belief-related and abstract inferences (e.g., [Evans, 2003; Goel et al., 2007](#)). Tsujii et al. presented problems with believable, unbelievable, and abstract content to participants and applied TMS to the SPL and inferior frontal gyrus (IFG); bilateral SPL stimulation disrupted performance on abstract and unbelievable inferences and stimulation of the left IFG (BA 45) impaired believable inferences. In another study, this group used

NIRS to study the same problems under time pressure; participants with enhanced right IFC activity performed better on unbelievable inferences. These findings support the main assumption of the dual-process theory: belief-related inferences rely on a heuristic system in left frontal cortical areas and abstract problems rely on a logical analytic system in the right superior partial cortex.

1.2. Preferred mental models in uncertain spatial reasoning

The theoretical background of our research is the mental model theory of reasoning ([Johnson-Laird, 2006](#)), which has its roots in deductive reasoning but can be applied to uncertain reasoning ([Bell & Johnson-Laird, 1998; Knauff, 2013; Walsh & Johnson-Laird, 2009](#)). The main assumptions of this theory are as follows. People do not reason according to formal rules of inference ([Rips, 1994](#)); instead, people use the meaning of premises to build a mental *integrated representation* of what might be true if the premises are true. "Integrated" means that the different pieces of information from the premise are not maintained as separate entities in the mind but rather that information is merged into a single representation that the reasoner holds temporarily active in their working memory; this integrated representation is the *mental model*. The mental model theory assumes that such mental models are spatially organized and thus are held in spatial working memory ([Knauff, 2013; Vandierendonck & De Vooght, 1997](#)). Inferences proceed in three steps. First, reasoners process the premises, understand what they mean, and mentally construct one possibility that agrees with this meaning of the premises, the initial mental model. Second, people use mental scanning processes to inspect the model for information not provided in the premises, leading to a preliminary conclusion. Third, people generate alternative interpretations of the premise to determine whether this preliminary conclusion holds in all possible models; if so, the conclusion must be true and is considered logically valid. This assumed process of generating alternative models indicates that the origin of the mental model theory lies in *deductive reasoning*. Classical logic defines that a conclusion is true if it holds in all possible models ([Byrne & Johnson-Laird, 1989; Johnson-Laird & Byrne, 1991](#)).

This is where the *PMM theory* starts. The core idea of the theory is that reasoners deal with the uncertainty of indeterminate premises by considering just one model and ignoring all other possibilities, leading to inferences that are not deductively valid. The core idea, i.e., people stick to an assumption as long as nothing contradicts, is also known from other areas of psychology ([Hoernig, Rauh, & Strube, 1993; Schank & Abelson, 2013](#)). In this vein, PMMs are those models of indeterminate premises that come to the reasoner's mind first and guide the inference as long as nothing contradicts it. Computer scientists call this process default reasoning, although these researchers make some other assumptions (e.g., [Reiter, 1987](#)).

The PMM theory makes clear predictions regarding which model is preferred over others. For instance, in our fruit example, the theory predicts that the model in the first line (1) is the PMM. People have difficulties considering the other model (2) even though it also agrees with the premises ([Ragni & Knauff, 2013](#)); this other model is the AMM. The PMMs of spatial descriptions are those constructed according to the principle that new objects are added to a model without disturbing the arrangement of those objects already represented in the model and thus the PMM is the model in which the cognitive system sacrifices adjacency in favor of outside insertion. The AMM, in contrast, is the model in which the cognitive system relocates a token in favor of immediate insertion of the token at hand; however, such AMMs are only considered if truly required by the task. For instance, if an AMM is presented, the reasoner must decide whether this model is consistent with a set of premises. In such tasks, the reasoner constructs

the PMM first, but the PMM does not match the presented model; therefore, AMM construction begins, though these AMMs are not constructed from scratch but instead by model *variation*. This process starts with the PMM and then changes the initial PMM model to obtain AMMs that are consistent with the premises. This model variation process is prone to error and requires additional executive processes. What happens if an IMM is presented, i.e., a model that does not agree with any possible interpretation of the premises? The reasoner attempts to map the PMM to the presented IMM (3, 4) recognizes that this match fails, and rejects the IMM as being inconsistent with the premises (Ragni & Knauff, 2013). Hence, this case is the easiest.

1.3. Tasks and hypotheses

Brain-imaging studies identify *correlations* between cognitive processes and cortical activity and indicate which brain areas are *sufficient* for the cognitive task. A problem with this technique, however, is that it remains unclear whether such activations are *necessary* for a specific cognitive function. Patient studies provide such information about the necessity of brain areas, but they have other problems. For instance, “natural” lesions are often not restricted to particular functional brain areas and are often difficult to precisely localize. Moreover, patient studies are often hindered by task heterogeneity and limited replicability (Shuren & Grafman, 2002).

TMS can elegantly bypass such problems since it makes it possible to explore *causal links* between a certain brain area and a specific cognitive function. Based on the reported findings from the literature, we assumed that the rSPL should play a causal role in uncertain reasoning with *belief-neutral, indeterminate relational premises*. Therefore, we applied TMS to this area and a control site, the so-called *vertex* (see below), which should not have any effect on reasoning.

We always presented four premises, each of which described the spatial relations between two objects, together resulting in a linear order of five objects. Next, we presented a linear order of these objects, and the participants had to decide whether this linear order was consistent with the premises. We assumed that participants solved these tasks by trying to match their internal mental model with the presented order of objects; however, all the problems were indeterminate, meaning that they did not provide enough information to construct a single consistent mental model. Based on the PMM theory, we assumed that people cope with this uncertainty by constructing a single PMM, although the premises allowed for multiple models. We therefore presented three types of linear orders: one that matched the PMM, one that matched an AMM, and one that did not agree with any possible model of the premises. Below, we refer to these three types of tasks as *PMMs*, *AMMs*, and *IMMs*, respectively. From a logical point of view, this terminology is not perfect, but we use it here since other formulations would render this report too complicated and circuitous; additional details are described in the Material and methods section. We used fruits and tools, for which no typical spatial arrangements exist (Knauff, 2013).

Table 2 summarizes our predictions. A “+” implies that we expected *more errors* under TMS stimulation than under vertex stimulation and a “0” means that we expected no effect of TMS stimulation compared to vertex stimulation. The PMM has a “+” because we predicted that PMMs are represented and processed in the rSPL. The AMM has a “+” because we expected that participants would construct the PMM but then vary it to obtain the AMM; this variation should rely, again, on neural computations in the rSPL. Overall, the AMM tasks should result in more errors regardless of whether TMS is applied to the rSPL or the vertex. For IMMs, we expected TMS to have no effect because the matches

Table 2

Predictions: Expected differences in errors for PMM, AMM, and IMM problems as a function stimulation site (SPL = superior parietal lobe) and the control condition (vertex).

| | TMS site | |
|-----|----------|--------|
| | rSPL | Vertex |
| PMM | + | 0 |
| AMM | + | 0 |
| IMM | 0 | 0 |

between IMMs and PMMs already fail for the first two objects in the models.

2. Material and methods

We used MagPro X100 (Magventure, Denmark) TMS equipment with a figure-eight coil for the stimulation (rTMS). During the experiment, 10-Hz biphasic TMS pulses were applied over 600 ms (six pulses); in previous studies, this frequency consistently modulated cognitive processing (Hartwigsen, Baumgaertner, Price, Koehnke, & Ulmer, 2010). The train of pulses was triggered 980 ms after the onset of the presented model. Stimulation was applied to the rSPL and the vertex as a baseline (control condition). Additional technical details are described below. Before the TMS experiment, all of the participants were scanned by a 3-Tesla scanner at the University Clinic Freiburg to precisely locate each individual's rSPL.

2.1. Participants

Twenty-nine participants took part in this experiment; all participants provided informed consent and were screened with the TMS-Screening Questionnaire (Keel, Smith, & Wassermann, 2001) for adverse reactions to TMS. Three participants were excluded from the study due to a mean performance below chance level; two additional participants were excluded due to technical errors. The remaining 24 participants (13 women, 11 men) were included in the data analysis (mean age: 22 years, range: 18–26 years). The study was approved by the Ethics Committee of the University Clinic Freiburg.

2.2. Reasoning problems

Each participant had to solve 72 relational reasoning problems, such as the fruit example given above (cp. **Table 1**). All of the problems consisted of four premises and five objects; the objects of the premises were either five types of fruit (apples, lemons, pears, bananas, or peaches) or five types of tools (hammers, drills, files, saws, and pliers). The objects were randomly assigned to a position in the premises, and the order in which problems were presented was random. All of the problems and instructions were presented in German. After the presentation of the four premises (cp. **Fig. 2**), participants had to decide, on a response box, whether the presented order agreed with the premises. The problems matched the PMM in one-fourth of the problems ($n = 18$), the AMM in one-fourth of the problems ($n = 18$), and the IMMs in half of the problems ($n = 36$); thus there were the same numbers of consistent and inconsistent models.

Half of the 72 problems were presented while the rSPL was stimulated and the other half during stimulation of the vertex (9 PMM, 9 AMM, and 18 IMM in each condition). Thus, the experiment had a 2×3 design with the within-subject factors stimulation site (rSPL, vertex) and problem type (PMM, AMM, IMM).

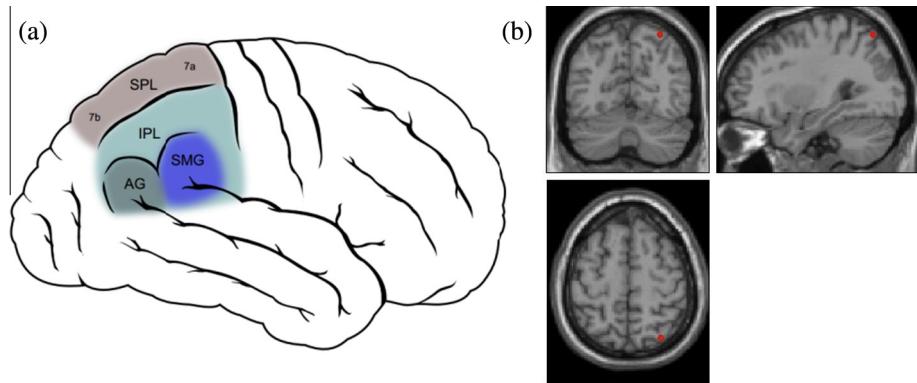


Fig. 1. (a) Sketch of the parietal cortex in the right hemisphere with four subregions: superior parietal lobe (SPL), inferior parietal lobe (IPL) including the angular gyrus (AG) and the supramarginal gyrus (SMG). (b) Localization of the superior parietal lobe (SPL 7A) for the right site stimulation. Images show a normalized structural brain image, red dots indicate the target region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

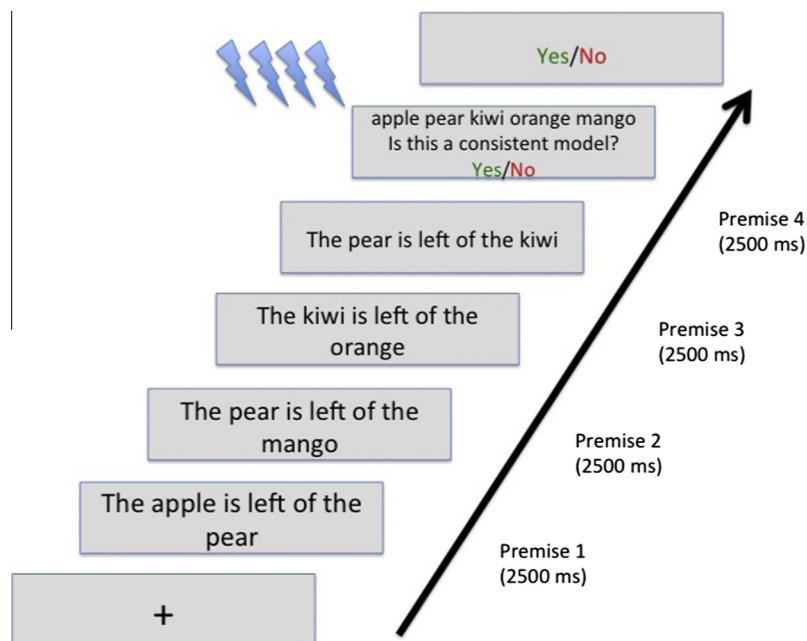


Fig. 2. Sequence and timing of one trial presentation.

2.3. Procedure

We conducted the study in two separate sessions. In the first session, participants filled out a questionnaire about their demographic information and completed a training session that included 20 practice trials; the presentation procedure was equivalent to the procedure during the TMS session. The results of the training session were used as a selection criterion: only those participants who performed better than chance for all three problem types were invited to take part in the TMS study. Participants also completed the Corsi block-tapping test, which is a standard method to measure individual differences in visuo-spatial working memory capacity (Kessels, van Zandvoort, Postma, Kappelle, & de Haan, 2000). In the classical version of the test, the subject is asked to mimic the researcher's actions as he taps a sequence of up to nine spatially separated but visually identical blocks. The researcher begins with just two blocks but then makes the task harder by tapping on more and more blocks until the subject's performance decreases. The maximum number of blocks that can be successfully repeated is called the Corsi Span and is approximately

5 for healthy participants (Kessels et al., 2000). We used a computerized version of the test that took about 10 minutes (PEBL, 2013). Many cognitive and brain-imaging experiments have indicated: (1) that performance on the Corsi test is related to the capacity of the visuospatial sketchpad (VSSP) within Baddeley's working memory theory (Baddeley, 2003, 2007) and (2) that the SPL is an important neural correlate of the VSSP (e.g., Wager & Smith, 2003; Wagner, Shannon, Kahn, & Buckner, 2005).

After participants successfully completed the training sessions and the Corsi test, they were invited to the second session, which was conducted in the TMS Lab of the Neurocenter Freiburg. First, the stimulation intensity was determined (see "TMS protocol"). Next, the coil was positioned either on the right parietal cortex or the vertex. The order of the stimulation sites was counterbalanced across participants (12 received SPL stimulation first and 12 received vertex stimulation first). The coil position was monitored by stereotactic navigation (LOCALITE TMS Navigator, Germany). Participants were then asked to complete the first half of the experiment, i.e., 36 problems. Participants pressed a button to start each trial (Fig. 2). The four premises, followed by the

PMM, AMM, or IMM, were successively presented for 2500 ms and separated by a blank screen that persisted for 1000 ms. Premises were presented centrally in black letters on a light gray computer screen. An answer symbol was presented simultaneously with the PMM, AMM, or IMM to indicate that an answer was required; the symbol disappeared as soon as a decision was made. Answers were submitted by pressing one of two buttons on a CEDRUS-button box.

In each problem, a 10-Hz pulse train was triggered 980 ms after the onset of the presentation of a possible order of objects. The onset asynchrony was determined by the length of the stimuli: 500 ms plus 20 ms times 24, which is the average number of letters of the premises (cf., Franzmeier, Hutton, & Ferstl, 2012). After 36 problems, the participants could take a short break while the TMS coil was repositioned at the second stimulation site. Afterward, the next 36 problems were presented as in the first part of the experiment. When the experiment was completed, the participant was debriefed and compensated with either 20 € or three course credits.

2.4. TMS protocol

The motor threshold was determined by measuring motor-evoked potentials (MEP). The individual resting motor threshold (rMT) was defined as the lowest stimulation intensity that elicited twitches in the hand. The rMT was determined using adaptive parameter estimation by sequential testing procedures that were based on the maximum-likelihood strategy for estimating motor thresholds (MTAT 2.0; <http://clinicalresearcher.org>). The stimulation intensity for TMS was defined as 100% of the individual rMT. The mean rMT of the 24 participants was 37% (range: 27–55%) of the stimulator's output strength. During the experiment, 10-Hz biphasic TMS pulses were applied over 600 ms (six pulses); this frequency modulates cognitive processing (Hartwigsen et al., 2010). The train of pulses was triggered 980 ms after the onset of the presentation of a possible order of objects. Stimulation was applied to the rSPL; the vertex was stimulated as a control condition (baseline).

2.5. Localization of the rSPL

Using the Anatomy Atlas (Eickhoff et al., 2005), the SPL 7A region was extracted as a region of interest (cf. Scheperjans, Eickhoff, et al., 2008; Scheperjans, Hermann, et al., 2008). This region of interest mask was transformed into the individual space (MNI to individual) and mapped to a high-resolution structural MRI scan of each participant that was collected with a 3-T Siemens TRIO scanner (Siemens, Erlangen, Germany) prior to the experimental session. The region of interest, as highlighted by the SPL 7A mask, was then chosen as the point of stimulation during the TMS experiment (Fig. 1b). The position of the TMS coil was determined and monitored via stereotactic navigation (LOCALITE TMS Navigator, Germany). During the stimulation, the participants' heads were stabilized with a chin rest and the coil was affixed onto a flexible arm.

3. Results

We compared the mean error rates between rSPL and vertex stimulation. A participant's response counted as an error if a consistent PMM or AMM was evaluated as inconsistent or if an IMM was evaluated as consistent. Because of the non-normal distribution and inhomogeneity of variances, we used non-parametric statistics, which are appropriate for assessing the significance of differences in within-subjects experiments (Siegel & Castellan,

1989). We also analyzed decision times, but did not find any reliable differences; therefore, we report only the error rates.

3.1. Overall differences between PMM, AMM, and IMM problems

We first analyzed the overall performance of participants, regardless of whether TMS was applied to the rSPL or the vertex. The overall error rate was 15.2% (standard deviation (SD) = 8.6). The rejection of the IMM was the simplest (11.2% errors), followed by verification of the PMM (14.6% errors) and verification of the AMM (23.8% errors). This trend was statistically significant (Pages-L, $L = 302$, $p = .02$) and replicated findings from previous experiments (Ragni & Knauff, 2013; Rauh et al., 2005). The planned pairwise comparisons were also significant after Bonferroni correction (one-tailed Wilcoxon signed-rank tests, PMM vs. AMM: $z = 1.8$, $p = .04$, $r = .26$; PMM vs. IMM: $z = 1.14$, $p = .13$, $r = .16$; AMM vs. IMM: $z = 2.34$, $p < .01$, $r = .34$).

3.2. Differences between PMM, AMM, and IMM problems during TMS stimulation

The reasoning errors for PMM, AMM, and IMM problems during rSPL and vertex stimulation are presented in Table 3. When presented with PMM problems, participants made more errors under rSPL stimulation than under vertex (control) stimulation; this difference was statistically significant (18.2% vs. 10.9%; one-tailed Wilcoxon signed-rank test, $z = 1.68$, $p = .046$, $r = .24$). When presented with AMM problems, participants also made more errors under rSPL stimulation than under vertex stimulation, but this difference was not statistically significant (26.3% vs. 21.3%; one-tailed Wilcoxon signed-rank test, $z = 1.03$, $p = .15$). For the IMM problems, we did not observe any difference between rSPL stimulation and control stimulation (one-tailed Wilcoxon signed-rank test, $z = 0.10$, $p = .92$).

3.3. Differences between participants within high and low VSSP spans

The Corsi test² revealed a mean VSSP span of 5.8 (SD = 0.8). In the next step, we computed several post-hoc tests for correlations among memory span, reasoning performance, and TMS effects. We found that performance was positively correlated with VSSP span: the higher the participants' VSSP span, the better their reasoning performance (Kendall's $\tau = .43$, $z = 2.61$, $p < .01$). For further analysis, we split the participants into two groups based on the mean VSSP span: a high VSSP group ($M = 6.4$, 12 participants) and a low VSSP group ($M = 5.1$, 10 participants). The high VSSP group reliably performed better than the low VSSP group (10% vs. 21.7% errors; one-tailed Wilcoxon rank-sum test, $z = 2.68$, $p = .003$), and the same pattern held true for PMM (8.9% vs. 21.2% errors; one-tailed Wilcoxon rank-sum test, $z = 2.04$, $p = .02$) and AMM problems (14.1% vs. 37.9% errors; one-tailed Wilcoxon rank-sum test, $z = 2.34$, $p = .01$). Interestingly, TMS on rSPL had a marginally significant effect on the PMM in the low VSSP group on error rates (rSPL 27.5% vs. vertex 15.0%; one-tailed Wilcoxon signed-rank test, $z = 1.55$, $p = .08$) but not the high VSSP group (rSPL 9.4% vs. vertex 8.3%; one-tailed Wilcoxon signed-rank test, $z = 0.16$, $p = .5$). This difference was less evident in the AMM problems for the high VSSP group (rSPL 17.7% vs. vertex 11%; one-tailed Wilcoxon signed-rank test, $z = 1.13$, $p = .13$) and the low VSSP group (rSPL 39.5% vs. vertex 36.2%; one-tailed Wilcoxon signed-rank test, $z = .41$, $p = .36$).

² The PEBL system did not record data from two participants.

Table 3

Empirical results: Mean percentages and standard deviations of errors for PMM, AMM, and IMM problems as a function stimulation site (rSPL = right superior parietal lobe) and the control condition (vertex).

| TMS site | | | Difference |
|----------|--------------|--------------|---------------------|
| | rSPL | Vertex | |
| PMM | 18.2% (1.64) | 10.9% (0.98) | 7.3% ($p = .046$) |
| AMM | 26.3% (2.37) | 21.3% (1.92) | 5.0% ($p = .15$) |
| IMM | 11.2% (4.03) | 11.2% (4.03) | 0% ($p = .92$) |

4. Discussion

We had three reasons for conducting this study. First, previous brain-imaging experiments found *correlations* between uncertain relational reasoning and neural activity in rSPL, but we wanted to explore whether these brain areas were actually *causally relevant* for uncertain relational reasoning. Patient studies pointed in this direction, but with TMS we have better control over the disrupting effects than we do in “natural” brain lesions, i.e., we can employ a within-subject design. Second, the majority of previous studies on human reasoning were concerned with *deductive* reasoning; we wished to explore what would occur in the brain if the inferences were *uncertain*. Therefore, we used indeterminate relational premises that were interpretable in more than one way. Third, the theory of PMMs was developed only recently. We already have empirical support for the theory from brain-imaging studies, as outlined above, yet, with TMS, we wished to create causal links between PMMs and the rSPL. Below, we discuss our findings in terms of these three research questions.

Is the rSPL necessary for reasoning about relations? Our findings indicate that the rSPL plays an essential part in reasoning about relations. Of course, in our study, we explored a specific subclass of relational reasoning. However, a transfer to certain relational reasoning has not yet been shown. Still, we think that both classes of tasks have certain neural and cognitive processes and resources in common. Support for this assumption comes from previous brain imaging studies about the rSPL showing its involvement in deductive relational reasoning with determinate premises (Goel & Dolan, 2001; Knauff, Fangmeier, Ruff, & Johnson-Laird, 2003; Knauff et al., 2002; for overviews see Prado, Van der Henst, & Noveck, 2010; Ragni et al., 2014). Our main finding is that TMS applied to the rSPL resulted in impaired uncertain relational reasoning performance and stimulation of the control site (the vertex) had no such effects; we interpret this to mean that the rSPL is indeed causally relevant for cognitive processes during (uncertain) reasoning about relations. If neural information processing in this area is disrupted, people have more difficulty solving (uncertain) relational reasoning problems, consistent with previous studies of neurological patients, which also related relational reasoning to areas in the rSPL (Goel & Dolan, 2003; Read, 1981; Tsuji et al., 2011; Waechter et al., 2013; Wendelken, Bunge, & Carter, 2007). These findings are also consistent with the theory of mental models (e.g., Goodwin & Johnson-Laird, 2005; Vandierendonck, DeVooght, Desimpelaere, & Dierckx, 1999; Vandierendonck, Dierckx, & DeVooght, 2004). According to this theory, people reason by constructing and manipulating spatially organized mental models. Therefore, the disruption of brain areas responsible for the integration and processing of spatial information from different modalities should impede reasoning, which is what we observed here.

Is the rSPL necessary for uncertain reasoning? Yes, it seems so, at least if the problems are relational and the premises are indeterminate. Of course, this conclusion is tentative and likely too strong to draw from a single experiment. On the one hand, this study is the first TMS study related to uncertainty in relational reasoning and it

is therefore remarkable that such indeterminate inferences are hindered if the neural processing in the rSPL is suppressed, in agreement with previous studies (Goel et al., 2009; Waechter et al., 2013); on the other hand, it is clear that this evidence should not be overgeneralized to other forms of thinking and reasoning. Conditional and syllogistic reasoning relies on a more complex cortical network and dealing with uncertainty in these sorts of inferences likely relies on other brain areas (e.g., Prado et al., 2011). Another critical point is that the rSPL is specifically involved in uncertain relational reasoning not because of the uncertainty but rather the relational character of the tasks, which certainly is more closely related to space than other forms of inference.

Do the present findings support the theory of PMMs? Yes, but our findings also raise new questions. Why do they support PMM theory? Well, we could show that the presented orders that agreed with the PMM were overall easier to verify as consistent, but when we applied TMS to the rSPL, reasoning with the PMM was more impaired than reasoning with other models; this finding is consistent with our predictions in Table 3. This result is interesting since it reveals that not all mental models are the same. If these models were identical, TMS should not have differentially affected PMMs and AMMs. PMMs seem to be different from AMMs not only cognitively but also in terms of their underlying neural computations. We believe that PMMs are likely the kind of models that are most intimately linked to the parietal cortex because PMMs are spatially represented and scanned by a spatial focus working on this representation (Ragni & Knauff, 2013).

The results for the IMMs are also quite clear. As we predicted in Table 3, these problems were not affected by TMS because when people read premises, they construct a mental model of what is true if the premises were true. Since our problems were indeterminate, reasoners simply constructed the PMM. If an order was then presented that was inconsistent with the PMM, this fact became immediately obvious. Participants simply had to compare the two objects of the order with the PMM to note that this match failed. According to the PMM theory, this process is sufficient to reject the order as inconsistent with the premises.

Why do our results raise new questions for the PMM theory? Our predictions were only partially supported for problems in which an order was presented that only agreed with the AMM. For these problems, we expected significant differences between the rSPL and control stimulations (see Table 3); we observed a trend in this direction, but the differences were not statistically significant. There are several possible explanations for the statistical insignificance of this difference. First, it might be simply a matter of test power ($n = 24$). Second, it is possible that TMS did not actually affect reasoning with AMMs. Consequently, this would mean that the AMMs were processed in different cortical areas than the PMMs. We do not think that this situation is plausible because it would disagree with many cognitive findings (Baker, Frith, Frackowiak, & Dolan, 1996; Burgess, Maguire, Spiers, & O’Keefe, 2001; Fangmeier & Knauff, 2009; Fangmeier, Knauff, Ruff, & Sloutsky, 2006; Oliveri et al., 2001; Postle, Stern, Rosen, & Corkin, 2000; Smith & Jonides, 1998). A third possible explanation for the insignificant difference among AMMs during the rSPL and control stimulations is that AMMs are disrupted in the same way as PMMs by TMS applied to the rSPL, but AMMs require additional processes in other brain areas that were not disrupted in our study (e.g., the PFC; see, e.g., Goel et al., 2009). This statement is likely true, but we believe that a fourth explanation, that there were VSSP capacity differences between the subgroups of our participants, is the most plausible. We admit that this account is more post-hoc and speculative; on the other hand, we maintain that examining the differences between subgroups of participants can be helpful to understand the complex results of reasoning experiments.

4.1. Differences between participants with high and low VSSP capacities

In previous studies, we scanned the brain activity of our participants during certain relational reasoning problems and also measured their VSSP capacities (Ruff, Knauff, Fangmeier, & Spreer, 2003). Interestingly, parietal activation correlated positively with reasoning performance but negatively with the participants' spatial skills; we explained our findings within a resource model in which people with lower abilities needed additional recourse to perform a task (Reichle, Carpenter, & Just, 2000), which can also explain the present results. As reported in the Results, we found that participants with higher VSSP capacities (Corsi span = 6.4) performed better on all tasks than participants with lower VSSP capacities (Corsi span = 5.1). This finding is not extremely surprising and again speaks to the role of spatial representation and processing in the VSSP during relational reasoning (e.g., Knauff et al., 2002; Oberauer, Weidenfeld, & Hörnig, 2006; Ruff et al., 2003; Vandierendonck & De Vooght, 1997); however, we also found that TMS of the rSPL affected the PMMs in the low VSSP group more significantly than in the high VSSP group, and this difference was less marked in the AMM problems. Our interpretation of this finding is that the processing of both PMMs and AMMs relies on VSSP capacity; however, the difference is that reasoning with PMMs requires less VSSP capacity than reasoning with AMMs, since only the latter calls for model variation. From this line of thought, it follows that reasoners with low VSSP capacities should reach their limits earlier than those with higher VSSP capacities; if TMS applied to the rSPL further limits reasoners' VSSP capacities, the reasoning of low VSSP participants should be limited even further and the high VSSP participants can better compensate for the TMS effect. We have shown that the effect of TMS in high VSSP participants increases from PMMs to AMMs because generating the AMMs requires additional VSSP recourses; the low VSSP participants did not exhibit this effect because the AMM tasks were more difficult without the disrupting effect of TMS. Therefore, we did not find an additional effect of TMS on the AMMs. One may speculate that we might have obtained a stronger effect of TMS on AMMs if we limited participation to those with high VSSP capacities.

Some of our conclusions need further empirical study. Other findings are more robust and agree with previous fMRI and patient studies; in particular, our research shows that the rSPL is not only correlated with but actually necessary for relational reasoning. Patient studies pointed in this direction, but we could support this further by a controlled suppression of the neural activity in rSPL within subjects. We also could identify differences between the preferred and alternative interpretations of uncertain premises. Further studies must explore how other brain areas contribute to uncertain reasoning with familiar and unfamiliar materials. We now briefly describe these open questions.

4.2. Questions for future research

The results of the current study establish a causal contribution of the rSPL in reasoning, but there are still many open questions. The first open question is related to the relatively modest effects of TMS on participants' performance on uncertain relational reasoning tasks. It is important to know that TMS by no means results in a blocking of brain areas but in a relatively moderate suppression in neural activity. Hence, the common understanding of TMS as temporal lesion is misleading (Ruff, Driver, & Bestmann, 2009). Moreover, for technical and safety reasons we used a stimulation paradigm in which the TMS signal was applied just for few milliseconds. However, we believe that longer stimulation interval might result in a more pronounced disruption effect. We will study this in future experiments.

The second open question is how individual differences in working memory span affect uncertain relational reasoning. Our study showed interesting differences between PMM and AMM in people with higher or lower WM span. However, more studies are needed to understand the connection between the PMMT and working memory capacity. This topic will also be part of our future research.

The third open question is related to the left PPC. Various studies reported bilateral activation of the PPC (cf., Knauff, 2009, 2013) without, however, specifying if the left PPC (angular gyrus and/or SPL) was also specifically involved in the reasoning process. Therefore, what is the role of the left PPC (cf. Franzmeier, 2013; Lau, Phillips, & Poeppel, 2008)? We will explore this subject with TMS in future studies.

The fourth open question is related to the distinction between reasoning with familiar and unfamiliar material. Goel et al. (2004) and Goel (2007) showed that the involvement of a linguistic system or visuo-spatial system can be systematically manipulated as a function of the content and context of the stimuli (Goel, Buchel, Frith, & Dolan, 2000; Goel & Dolan, 2003; Goel et al., 2004). The framework of Goel et al. (2007) proposes that a left lateralized frontal-temporal language system processes familiar materials and a bilateral parietal visuo-spatial system processes unfamiliar or incoherent material. With this distinction, Goel refers to the suggestion that the frontal-temporal pathway corresponds to a heuristic system and the parietal pathway corresponds to a formal or universal system (Goel, 2003, 2007). The basic idea is that reasoning about familiar situations utilizes situation-specific heuristics in a frontal-temporal system; these heuristics are based on background knowledge and experience. In contrast, for abstract inferences, no such heuristics exist; therefore, a belief-unrelated formal system in the parietal cortex is used. In our study, we only used problems for which our participants did not have any background knowledge. There are no more or less typical orders of fruits or tools; they are all equally likely. Therefore, it is plausible that TMS on the rSPL negatively affected reasoning performance. Together with the results of Waechter et al. (2013), our results show that the maintenance and manipulation of mental models relies on neural computations in the parietal cortex. We will study the differences between familiar and unfamiliar materials in future TMS studies.

A final question is related to the executive processes involved in reasoning and how TMS of the frontal cortex affects reasoning performance. Our previous research on model variation and many brain-imaging studies on executive functioning led to the assumption that disrupting the function of people's prefrontal areas should result in massive decrements in their reasoning abilities (Fangmeier et al., 2006; Knauff, 2013). Our present study was concerned with reasoning with spatial relations. Such problems are likely more closely linked to spatial processing in parietal cortical areas than other forms of reasoning, such as conditional (with "if," and "then") or syllogistic reasoning (with quantifiers such as "all," "some," "none," etc.). Brain-imaging studies on these forms of human reasoning produced quite complex patterns of activation, distributed over several cortical areas (Goel, 2007; Prado et al., 2011) other than the SPL. In our future studies, we will extend our research to these other forms of uncertain reasoning. This future work will also show how universal our current findings are and which role the SPL plays in other forms of thinking and reasoning. The present study at least demonstrates that this area is truly used in uncertain reasoning with ambiguous spatial premises and that its disruption hinders people's reasoning.

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