Reasoning and working memory: common and distinct neuronal processes

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Abstract

The neuronal processes underlying reasoning and the related working memory subsystems were examined with functional magnetic resonance imaging (fMRI). Twelve volunteers solved relational reasoning problems which either supported a single (determinate) or several alternative solutions (indeterminate). In a second condition, participants maintained the identical premises of these problems in working memory without making inferences. Although problems were presented in auditory format, activity was detected for both reasoning and maintenance in a network comprising bilaterally the secondary visual cortex, the posterior cingulate cortex, and the medial anterior frontal cortex. In direct comparisons, reasoning was associated with stronger dorsolateral and medial prefrontal activation than maintenance, whereas maintenance led to stronger lateral parietal activation than reasoning. Participants' visuo-spatial abilities ("Block Design" score) covaried positively with behavioral performance and negatively with activity of the precuneus for reasoning, but not for maintenance. These results support the notion that relational reasoning is based on visuo-spatial mental models, and they help to distinguish the neuronal processes related to reasoning itself versus to the maintenance of problem information in working memory.
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1. Introduction

Recent investigations have identified the brain networks active during various forms of reasoning, depending on characteristics of the reasoning tasks or the specific problems under study [24–26,37,43,45,52,54]. Despite this growing knowledge about differences in the brain mechanisms *between* types of reasoning, little is known about the processes *within* each of the tasks. That is, previous studies have not empirically distinguished activations due to "pure" reasoning processes from activations connected to more elementary processes, such as semantic processing of premise information or the maintenance of the problem information in working memory.

The aim of the present study was to disentangle the neuro-cognitive mechanisms underlying reasoning and the related working memory subsystems. Two questions were of interest: First, which cortical areas are involved in both reasoning and maintenance, pointing to neuro-cognitive processes required mainly for representing the problem information in working memory? Second, which areas are exclusively active during reasoning, indicating "pure" reasoning processes on top of the mere maintenance and storage of problem information? In the following, we will explain the form of reasoning employed in the present study and give a brief overview of theoretical accounts and neuro-cognitive investigations on this topic. Then we describe an fMRI study in which the neuronal correlates of reasoning and maintenance in working memory were examined. In the discussion, the results are related to cognitive theories of reasoning and to findings concerning the neuronal correlates of working memory. The paper concludes with some general thoughts on a neuro-cognitive theory of human inference.

In the study, we employed *relational reasoning* problems which are essential to daily life. We focused on problems with a spatial content, since their behavioral underpinnings are well understood [18,29,30]. The term *relational reasoning* usually refers to the processing of information about the relation between objects, with the aim of generating new

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information that is not explicitly available. It is required when solving spatial problems such as:

- the fork is to the left of the plate;
- the glass is to the left of the fork;
- which relation holds between the glass and the plate?

The first two sentences of such problems are linked by a common term ("fork"); they are referred to as premises, while the third sentence is called conclusion.

Two major theoretical positions have emerged that describe how people reason about such problems. Proponents of theories based on *formal rules* claim that people solve reasoning problems by means of a set of inference rules. These rules are applied sequentially to a language-based representation of the problems or their logical form. Thus, the basic assumption of this approach is that reasoning is a mainly *linguistic* process, mediated by left-hemisphere neuronal systems involved in language processing [7,62,65]. This account is directly challenged by the theory of *mental models*. It assumes that people reason by means of visuo-spatial models of the "state of the affairs" described in the premises. Mental models capture in a structurally isomorphic representation one situation that is possible, given that the premises are true. In this framework, reasoning is conceptualized as a three-stage process in which individuals first construct unified mental models, then inspect them for the desired relation to find a putative conclusion, and finally search for counterexamples that satisfy the premises but refute this putative conclusion. If no such counterexample is found, the conclusion is considered valid [29,30]. As these hypothesized operations mainly depend on *visuo-spatial* processes, reasoning should be mediated by occipito-parietal cortices, possibly with a right-hemisphere prevalence [27, 29,40].

Behavioural studies on relational reasoning have generally supported the predictions of the theory of mental models. For instance, reasoners are less prone to errors when solving relational reasoning problems consistent with a single layout (*determinate problems*) than problems for which such a unique layout does not exist (*indeterminate problems*). In an experiment by Byrne and Johnson–Laird, 70% of the responses were correct for problems consistent with a single arrangement, while only 46% of the responses were correct for problems supporting multiple layouts [11,30]. Since for these problems the number of rule applications was not related to problem difficulty (as assumed by the rule account), the results can be seen as evidence that reasoners actually construct and inspect mental models in order to derive a conclusion for the problem. The logic behind this approach is that indeterminate problems should be more difficult if people employ mental models, since considering more than one model has higher storage and processing demands than the construction of a single arrangement. Alternatively, people may reduce this complexity by employing so-called *initial* or *preferred* mental models [30,32,60]. In this case, however, they have to maintain additional details of the premise information in working memory in order to derive other possible arrangements [49].

The notion that reasoning by mental models is processed in visuo-spatial *working memory* is also emphasized by studies using the so-called dual-task paradigm. In these experiments, participants are required to solve reasoning problems while simultaneously carrying out tasks that selectively occupy the capacity of one of the three proposed subsystems of working memory, i.e. the phonological loop (PL), the visuo-spatial sketch pad (VSSP), or the central executive (CE) [2,3]. Three studies found significant interference of tasks that occupied the VSSP and the CE with relational reasoning, as predicted by the theory of mental models [31,35,71]. In addition, the results of one study indicated that visuo-spatial processes are already engaged at the very early stage of understanding the single premises [71]. Finally, recent fMRI studies also support the mental model theory of reasoning. These studies found activity in a bilateral network comprising occipital, parietal, and dorsolateral frontal brain regions during relational reasoning, indicating visuo-spatial processing [25,33,37]. However, the precise contributions of the working memory processes underlying this phenomenon are not yet understood.

In the present study, we performed fMRI while volunteers either solved spatial relational reasoning problems or merely maintained the premises in working memory without making inferences. For both sorts of problems, an equal number of problems consistent with one, three, or five spatial layouts was used [32,60]. To examine the influence of individual differences in skill and strategy use, the participants were tested after the experiment with the "Block Design Test" of the German equivalent to the Wechsler Adult Intelligence Scale (HAWIE-R) [69], and they were also interviewed about the strategies they applied to solve the problems.

2. Methods

2.1. Participants

Twelve male right-handed German native speakers (mean age 24.0 years, S.D. 3.21 years) with normal or corrected-to-normal vision (contact lenses) and normal audition participated in the experiment. None of the volunteers had any history of neurological or psychiatric disorders, or of significant drug abuse. All subjects gave their informed consent prior to the participation in the study, and all procedures administered complied with both university and hospital ethical approval.

2.2. Materials

The materials consisted of reasoning and maintenance problems. The *reasoning problems* were 24 relational inferences and included the following relations: left of, right of, overlaps from the left, overlaps from the right, meets from

the left, meets from the right, lies inside of, and lies outside of. These spatial-relational expressions have been used successfully in earlier experiments [32,37,60]. All problems described the spatial relation between coloured geometrical objects in order to avoid effects of content or different ease of imagination for different objects. An example for a reasoning problem is:

Premise 1: The red interval lies to the right of the green bar.
Premise 2: The green bar lies to right of the blue rectangle.
Conclusion: The red interval lies to the left of the blue rectangle?

The experiment employed an *inference–verification paradigm* requiring the subjects to evaluate the correctness of a conclusion presented after two premises. The order of the three colour names (red–green, green–blue) was constant across all problems. The three object terms "interval", "bar", and "rectangle" (German: "Intervall", "Band", and "Rechteck") were used as synonyms, and their position and colour association was fully permutated across the problems with the restriction that each problem contained all three object names in a fixed association with one position and colour. An equal number of the problems were consistent with one, three, or five mental models, as implemented in previous studies [32,60].

The 24 *maintenance problems* required subjects to compare the premises with a third sentence in terms of their exact verbal content. Valid and invalid maintenance problems employed the premises of invalid and valid reasoning tasks, respectively. In place of the conclusions, valid maintenance problems contained repetitions of one of the two premises, while invalid problems repeated one of the premises with a different colour–object association for all three objects. This strategy was chosen to ensure that subjects had to process the exact linguistic detail of the sentences. The maintenance problem related to the inference given above would thus yield the valid third sentences:

The red interval lies to the right of the green bar

or

The green bar lies to right of the blue rectangle

or either of the invalid third sentences:

The red rectangle lies to the right of the green interval

or

The green interval lies to right of the blue bar.

Half of the problems repeated the first premise, and repetition of the first or the second premise was permutated across the problems consistent with a different number of mental models and the valid and invalid problems.

All sentences of the reasoning and maintenance problems were recorded as audio files spoken in the same voice, edited for similar length (between 3.9 and 4.0 s), and normalized for loudness and peak gain.

2.3. Experimental design

Problems were presented in a blocked design with four separate runs. Each run contained six blocks with one problem pair of each of the problem types (i.e. reasoning or maintenance problems consistent with one, three, or five mental models). This strategy accounted for any fluctuations of scanner sensitivity across runs which thus equally affected all types of problems. The problem pairs were randomly determined for each problem type and they remained constant throughout the whole experiment for all participants. The four pairs of each problem type were randomly assigned to the runs of each subject, and the order of the problem pairs within all runs was also randomly determined.

Each problem block consisted of the presentation of six sentences (4 s each) interleaved with silent breaks (6 s each) during which scanning was performed. The hemodynamic response was thus sampled in the absence of task-related auditory input. Between two of the problem blocks, a rest interval of similar length (60 s) was included, which differed from the experimental block only in the lack of problem presentation. During this rest interval, a white letter was displayed (drawn with a thin line of one pixel strength, visual angle of 2°), identifying the following problem pair as reasoning (S) or maintenance (E). The letter remained visible on the screen (background colour light grey) for the whole course of the rest interval and the problem presentation. Participants responded to the problems by button press in the response interval after the presentation of each conclusion. In order to prepare subjects for the beginning of the next problem, the letter on the screen briefly disappeared one second before the end of each response interval during both the problem and the rest blocks. Scanning was always performed before the letter disappeared, so that participants did not receive any correlated visual input during image acquisition.

2.4. Experimental procedures and scanning techniques

In a study-phase prior to instruction about the neuroimaging experiment, participants completed a computerized training of the relational terms used in the problems. This ensured they had understood each term well enough to define it correctly on three occasions. Participants were then instructed on the procedure of the experiment, and they completed a training experiment in order to reduce effects of novelty and strategy learning inside the scanner. The identical conditions, problems, and time course as in the following neuroimaging experiment were used. For reasoning problems, subjects were required to evaluate whether the relation between the objects described in the conclusion was consistent with the information in the premises. For maintenance problems, participants were asked to evaluate whether the third sentence

was an identical repetition of one of the two premises or whether it was different in terms of its exact verbal content.

Inside the scanner (1.5 T Siemens VISION), the participants' head position was fixed in the head coil, and a mirror system was placed on the coil so that participants could see a projection screen mounted on the rear of the scanner bore. Visual stimuli were projected onto this screen using a video beamer and professional presentation software [72]. Reasoning and maintenance problems were presented in auditory format via the headphones, and participants responded to them by pressing two buttons of an MR-compatible response box with their right index and middle finger ("yes" and "no" responses, respectively). Responses were recorded by the program, and response times were automatically calculated from the end of the presentation of the conclusion. The presentation of each stimulus pair was synchronized with the TTL-pulse emitted by the scanner at the beginning of each functional measurement.

Functional images were collected with a gradient-recalled echo-planar imaging (EPI) sequence, allowing the sampling of 30 parallel slices effectively covering the whole brain (TR: 10.1 s, TE: 66 ms, FOV: 256 mm × 256 mm, 2 mm × 2 mm in plane resolution, 4 mm slice thickness). Seventy-four functional image volumes were collected in each of the stimulus runs lasting 748 s.[1] Two rest scans were collected in the beginning of each run in order for T1-effects to stabilize, and these images were discarded from further analysis. At the end of the experiment, a functional EPI image with 40 slices and a sagittal T1-weighted magnetization-prepared rapid-acquisition gradient echo (MP-RAGE) image of the entire brain (160 slices, TR: 40 ms, TE: 6 ms, FA: 40°, FOV: 256 × 256 mm, voxel size: 1 mm × 1 mm × 1 mm) were acquired for purpose of co-registration and normalization during image preprocessing.

After the experimental session, the participants were tested with the "Block Design Test" of the German equivalent to the Wechsler Adult Intelligence Scale (HAWIE-R) [69], and they underwent a semi-structured interview in order to investigate the subjective impression of the strategies they had chosen to solve the problems. The focus of this interview was on whether they employed verbal or visuo-spatial strategies, and on whether they maintained the premises in separate or integrated representations.

2.5. Image preprocessing

All images were preprocessed and analyzed with the software Statistical Parametric Mapping 99 (SPM99) [67]. Functional and anatomical images were reoriented so

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[1] Since the synchronization of the scanner and the presentation software had failed on a few occasions, the rest intervals in a total of nine experimental runs contained one or two additional functional image volumes. These additional image volumes (always the first images acquired during the respective rest intervals) and the remaining images associated with the resulting incomplete last problem of the run (two or one) were discarded from further analysis.

that the anterior commisure corresponded to the origin of the three-dimensional standard coordinate system used in SPM99. However, note that all coordinates used to describe the results of the experiment correspond to the system originally introduced by Talairach and Tournoux [43,68]. The functional images collected during one run were subsequently realigned and corrected for motion in the scanner with the two-step realignment procedure embedded in SPM99. Translation and rotation corrections did not exceed 2.9 mm and 2.5° for any run. Each subject's anatomical image series was subsequently co-registered with the 40-slice EPI image volume collected at the end of the experiment. The mean images of the runs and all other functional images were then co-registered with the 40-slice EPI image volume. Parameters for spatial normalization were determined from the anatomical image volumes collected for each subject, and they were applied to the respective subject's functional image volumes. A new set of normalized functional images was created for which the original spatial resolution of the EPI volumes was interpolated from 2 mm × 2 mm × 4 mm to an isotropic voxel size of 3 mm³. The realigned and normalized images were finally smoothed with a 6 mm full width at half maximum (FWHM) Gaussian kernel.

2.6. Model specification and statistical inference

The hemodynamic response to the experimental cycle was modeled with a fixed-response box-car function, which was convolved with the canonical hemodynamic response function. Low-frequency confounds were excluded from the model with a high-pass filter of twice the experimental run's length (corresponding to 144 × TR). Variations in global signal intensity were not removed because of the danger of producing spurious local changes in the direction opposite to any change in global signal. The function contained for each stimulus run the appropriately placed models of the hemodynamic response to the problems belonging to the six conditions (reasoning or maintenance problems with one, three, or five possible mental models). The six sets of realignment parameters for each run were included in the model as covariates, to account for undesired effects of head movement. On the rare occasions of co-linearity of two realignment parameter sets (correlation $P > 0.80$), only the set which was less correlated with the other four parameter sets was included as a covariate.

The parameter estimates derived from the function were used for statistical analysis of brain activation differences between the experimental conditions, using Statistic Parametric Maps (SPMs) and the framework of the general linear model (GLM) implemented in SPM99. The following linear contrasts (subtractions) were specified:

1. reasoning versus rest;
2. maintenance versus rest;
3. reasoning versus maintenance;
4. maintenance versus reasoning;

5. indeterminate reasoning problems (three and five models pooled) versus determinate reasoning problems.

The covariation of task-related brain activity with the participants' visuo-spatial skills was examined with separate contrasts within the same model. The parts of the contrast vectors 1–4 corresponding to the images acquired for each specific subject were multiplied with this subject's mean corrected Block Design score (individual score − mean of all scores). These four new contrasts thus yielded all areas that showed, for the respective contrast, a linear increase in activity with increasing individual Block Design score. Negative covariations (decreasing activity with increasing Block Design score) were assessed by the negative inversion of the contrast vectors (i.e. multiplication with −1).

Given the engagement of many different processes and the extended time-scale of measurement in the Block Design, all inferences were performed at the cluster level ($P < 0.05$ corrected for multiple comparisons across the whole brain) [22].

3. Results

3.1. Behavioural data

3.1.1. Performance measures

The percentage of correct responses and the response times to reasoning and maintenance problems are given in Table 1. All statistical analyses were performed at an alpha level of 0.05 (two-tailed). Participants' responses to the reasoning problems were correct significantly less often than to the maintenance problems, Wilcoxon test, $z = 2.84$, $P < 0.01$, and reasoning was associated with significantly higher response latencies, Wilcoxon test, $z = 2.82$, $P < 0.01$. As expected, the accuracy in the maintenance tasks was not affected by the number of possible mental models (84.4, 85.4, and 86.5% correct responses for one, three, and five models, respectively), Friedman analysis of variance, $F = 0.68$, $P = 0.71$. The response latencies were also not affected by the number of models (1978, 2022, and 2045 ms, for one, three, and five models, respectively), Friedman analysis of variance, $F = 2.00$, $P = 0.37$. In contrast, the participants responded correctly less often to reasoning problems supporting one model as compared to problems with three and five mental models, which did not differ in accuracy (51.0 versus 70.9 versus 80.3%, respectively), Friedman analysis

Table 1
Mean accuracy (%, correct responses) and mean response latencies (ms) to reasoning and maintenance problems ($N = 12$)

	Task	
	Reasoning	Maintenance
Accuracy	67.3 (13.4)	85.4 (15.8)
Latency	2474 (650)	2015 (285)

Standard deviations are given in parentheses.

of variance, $F = 12.95$, $P < 0.01$. However, there was no significant effect for the response times to these three problem types (in order 2451 versus 2421 versus 2549 ms), Friedman analysis of variance, $F = 1.17$, $P = 0.56$.

3.1.2. Block Design Test

The spatial-constructive intelligence [69] of all subjects was within the normal to superior range (mean value equivalent to an IQ of 114, S.D. equivalent to 15 IQ points, lowest value equivalent to an IQ of 103). For the reasoning problems, the number of correct responses per subject showed a significant positive correlation with the participants' Block Design score, $r = 0.76$, $P < 0.01$, while the mean response times showed only a non-significant negative correlation with this index, $r = -0.33$, $P = 0.29$. For the maintenance problems, the corresponding correlations pointed in a similar direction, but both did not reach statistical significance, $r = 0.54$, $P = 0.07$ and $r = -0.47$, $P = 0.12$.

3.1.3. Interview

All subjects reported having used a visuo-spatial strategy for solving the reasoning problems. They reported having integrated the three objects into a single model or image, and differences between subjects were just present in the level of detail of these images (e.g. whether they explicitly contained all three colours or not). For the maintenance problems, most subjects reported having used a mixed strategy relying on images and abstract tokens or letters to represent the three objects, with some subjects also relying on just one of these two forms of representation by self-report.

3.2. Neuroimaging data

3.2.1. Reasoning and maintenance versus rest

In comparison with rest, reasoning elicited activity in bilateral middle occipital gyri, bilateral posterior cingulate, bilateral medial frontal gyrus, the precentral gyri of both hemispheres, and parts of the right parahippocampal gyrus. No clear hemispheric lateralization of activations could be detected; all regions except the parahippocampal gyrus were activated bilaterally. The contrast of the images acquired during maintenance and rest revealed activation in a comparable network, which overlapped with that found active during reasoning in bilateral visual association cortex, bilateral posterior cingulate, and bilateral medial frontal gyrus. The clusters in the latter two brain regions were more extensive for maintenance than for reasoning, while the occipital activation was more marked for reasoning than for maintenance and also extended into the cuneus and precuneus. Note that this medial occipital activation was located clearly superior to the calcarine sulcus containing the primary visual cortex.[2]

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[2] Visual inspection of the contrasts reasoning versus rest and maintenance versus rest separately for each participant (threshold $P = 0.001$ uncorrected for multiple comparisons) revealed that 9 out of the 12 participants showed reasoning-related activity in occipital cortex, while 8 participants showed such activation during maintenance.

Table 2
Activation clusters detected for the contrasts reasoning vs. rest, maintenance vs. rest, and the conjunction of reasoning and maintenance vs. rest

Location	Z-score	Size	Talairach coordinates		
			X	Y	Z
Reasoning vs. rest					
Occipital					
L middle occipital gyrus (BA 18)	6.06	96 Voxels***	−30	−93	2
R middle occipital gyrus (BA 18)	4.77	51 Voxels***	33	−87	7
B cuneus	4.23	49 Voxels***	−12	−86	26
Parietal					
L posterior cingulate (BA 31)	4.53	18 Voxels**	−6	−52	11
B precuneus	4.28	16 Voxels*	−3	−73	23
Frontal					
L precentral gyrus	4.77	43 Voxels***	45	−10	39
R precentral gyrus	4.40	17 Voxels*	−39	−13	34
B medial frontal gyrus	4.02	25 Voxels**	−6	53	8
Temporal					
R parahippocampal gyrus	4.02	16 Voxels*	27	−18	−14
Maintenance vs. rest					
Occipital					
L middle occipital gyrus (BA 18)	5.11	21 Voxels*	−30	−90	5
R inferior occipital gyrus	4.18	21 Voxels*	33	−88	−3
Parietal					
B posterior cingulate gyrus	4.69	126 Voxels***	3	−54	22
Frontal					
B medial + superior frontal gyrus (BA 10)	4.78	53 Voxels***	−6	59	14
B medial frontal gyrus (BA 10)	4.06	35 Voxels***	3	47	14
Conjunction: reasoning and maintenance vs. rest					
Occipital					
L middle occipital gyrus (BA 18)	8.15	123 Voxels***	−30	−90	5
R middle occipital gyrus (BA 18)	6.33	73 Voxels***	33	−88	7
Parietal					
B posterior cingulate gyrus (BA 29)	5.05	106 Voxels***	−6	−49	8
	4.34	17 Voxels*	3	−45	33
Frontal					
B medial + superior frontal gyrus	5.77	211 Voxels***	3	47	14

Note: SPM(Z)s were thresholded for height at Z = 3.09, and for spatial extent at $P < 0.05$ corrected for multiple comparisons. Location, Z-score, and Talairach coordinates refer to the peak voxel of the cluster. The correspondence of this voxel to Brodmann areas is only established when applicable; however, note that localization can only be performed at the level of the whole cluster. L: left; R: right; B: bilateral.
 * $P < 0.05$, corrected for multiple comparisons across the whole brain.
 ** $P < 0.01$, corrected for multiple comparisons across the whole brain.
 *** $P < 0.001$, corrected for multiple comparisons across the whole brain.

In order to directly examine the overlap of the activation patterns, a conjunction analysis was calculated which displayed all areas active during *both* reasoning and maintenance, while the activation present during only one of the two cognitive activities was excluded.[3] In congruence with

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[3] For this purpose, a new contrast image was calculated from the comparison of the images acquired during both experimental conditions and those acquired during rest (thresholded at $P < 0.05$ corrected for multiple comparisons, cluster-level inference). This contrast image was then masked with the contrast images calculated for reasoning versus rest and maintenance versus rest (both initially thresholded at $P = 0.05$ uncorrected for multiple comparisons), so that only regions active in *both* single contrasts were included in the results of the conjunction contrast. Note that this analysis is not a conjunction analysis in the strict sense of the word, for which an intersection SPM(*T*) is calculated for the single contrasts in order to perform statistical inference at the voxel level only.

the visual inspection of the single contrasts, the conjunction of reasoning and maintenance activated bilaterally parts of the middle occipital gyri, the posterior cingulate, and the medial and superior frontal gyri. Due to the increased statistical power of this contrast, these clusters were larger and associated with higher Z-values than those found for the single contrasts. Table 2 and Fig. 1 (top) summarize the activations resulting from the contrasts of reasoning or maintenance versus rest.

3.2.2. Reasoning versus maintenance

As displayed in Table 3 and Fig. 1 (bottom), reasoning was associated with more activation than maintenance in anterior cortical areas, comprising parts of the right anterior cingulate cortex (ACC) and the medial frontal gyri, bilaterally the
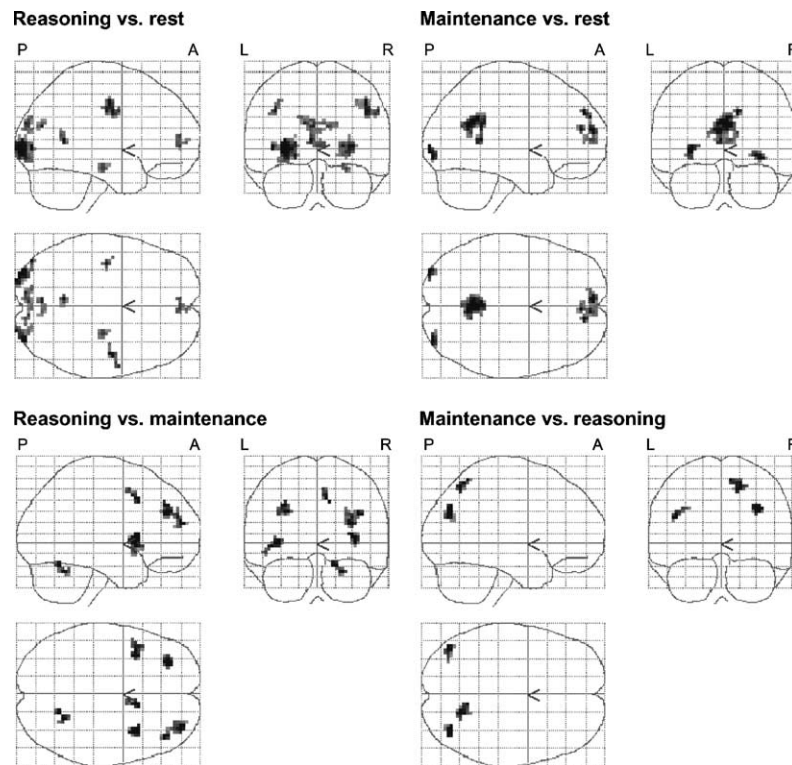
Fig. 1. SPM(Z)s for the contrasts reasoning vs. rest, maintenance vs. rest, reasoning vs. maintenance, and maintenance vs. reasoning. Z-values were transferred to an arbitrary gray scale and projected onto saggital, coronal, and transverse sections of a standard template brain. The SPMs were thresholded for height at $Z = 3.09$, and for spatial extent at $P < 0.05$ corrected for multiple comparisons across the whole brain. L: left hemisphere, R: right hemisphere, A: anterior end, P: posterior end.

Table 3
Activation clusters detected for the contrasts reasoning vs. maintenance and maintenance vs. reasoning

Location	Z-score	Size	Talairach coordinates		
			X	Y	Z
Reasoning vs. maintenance					
Frontal					
R anterior cingulate/medial frontal gyrus (BA 32)	4.49	18 Voxels*	9	14	38
L middle frontal gyrus (BA 9)	4.16	31 Voxels***	−27	42	26
R middle frontal gyrus	4.14	54 Voxels***	30	56	14
Temporal					
L insular cortex/superior temporal gyrus (BA 38)	4.58	38 Voxels***	−36	12	−1
R insular cortex	4.49	31 Voxels***	36	12	2
Cerebellum					
R posterior + anterior lobe	4.24	22 Voxels***	18	−59	−15
Maintenance vs. reasoning					
Parietal					
R inferior parietal gyrus (BA 7)	4.47	23 Voxels**	36	−71	34
R precuneus	4.03	30 Voxels**	15	−59	50
Temporal					
L middle temporal gyrus (BA 39)	4.67	23 Voxels**	−42	−71	28

Note: SPM(Z)s were thresholded for height at $Z = 3.09$, and for spatial extent at $P < 0.05$ corrected for multiple comparisons. Location, Z-score, and Talairach coordinates refer to the peak voxel of the cluster. The correspondence of this voxel to Brodmann areas is only established when applicable; however, note that localization can only be performed at the level of the whole cluster. L: left, R: right, B: Bilateral.

  * $P < 0.05$, corrected for multiple comparisons across the whole brain.

  ** $P < 0.01$, corrected for multiple comparisons across the whole brain.

  *** $P < 0.001$, corrected for multiple comparisons across the whole brain.

middle frontal gyri, and bilaterally the insular cortices. The cluster of ACC/medial frontal activation was located anterior to the areas known to be involved in mere preparation and execution of motor responses, in close proximity to an area previously found active during spatial working memory [55]. The activation clusters in the middle frontal gyri were located entirely superior to the inferior frontal sulcus and thus mainly in areas classified as dorsolateral prefrontal cortex (DLPFC) [21]. Parts of the cluster in the right hemisphere also extended into more anterior regions. However, despite the less precise localization power of the cluster-level analysis, this pattern of prefrontal activation was clearly distinct from the pattern found for the contrast of reasoning or maintenance versus rest.

3.2.3. Maintenance versus reasoning

Maintenance led to more activity than reasoning in the right inferior parietal gyrus, the right precuneus, and an area in the junction of the left middle temporal and inferior parietal gyrus (see Table 3 and Fig. 1, bottom). Note that this latter area was clearly posterior and inferior to the posterior temporal language region located in parts of the planum temporale, superior temporal gyrus, and supramarginal gyrus [75].

3.2.4. Visuo-spatial skills

The brain activation detected for the contrast reasoning versus rest was significantly modulated by the participants' visuo-spatial skill. As shown in Fig. 2, a cluster in the precuneus (peak coordinates: $x = 0$, $y = -62$, $z = 36$; cluster size 33 voxels) displayed a negative covariation with the participants' Block Design score. The higher the
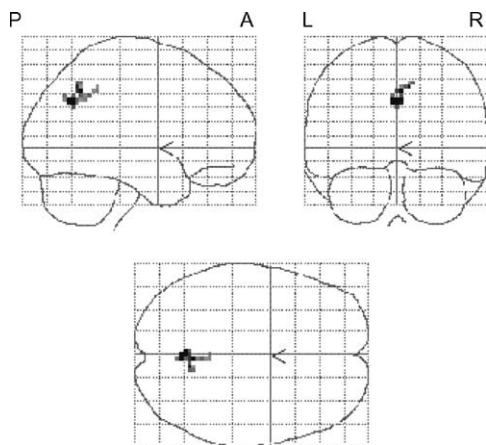

Fig. 2. Activity in the precuneus covaries negatively with visuo-spatial skills during reasoning. The figure displays the SPM(Z) for the contrast reasoning vs. rest, modulated by the subjects' mean corrected Block Design score. Z-values were transferred to an arbitrary gray scale and projected onto saggital, coronal, and transverse sections of a standard template brain. The SPM was thresholded for height at $Z = 3.09$, and for spatial extent at $P < 0.05$ corrected for multiple comparisons across the whole brain. L: left hemisphere, R: right hemisphere, A: anterior end, P: posterior end.
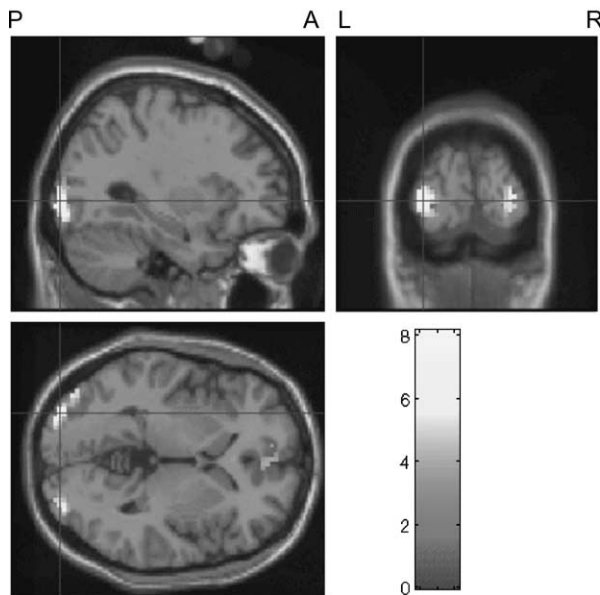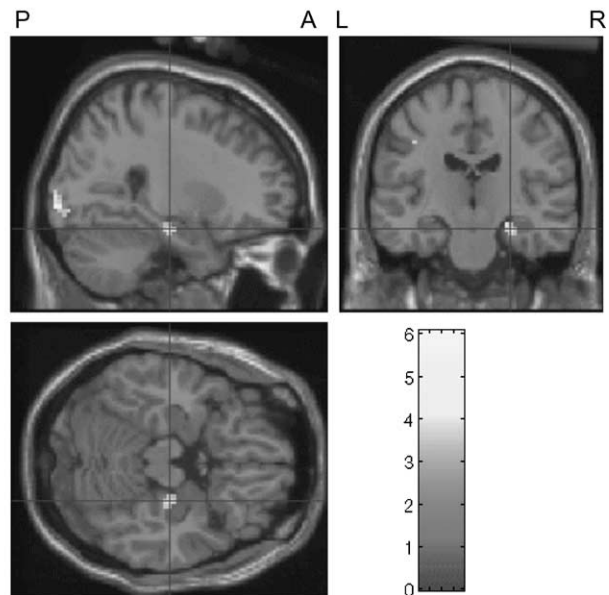
visuo-spatial skill, the less activation was measured in that area. No other areas displayed such a relationship, and no significant covariations were detected for the contrasts of maintenance versus rest, reasoning versus maintenance, and maintenance versus reasoning.

3.2.5. Determinate versus indeterminate problems

The contrasts between determinate and indeterminate reasoning problems did not reveal any significant differences. Visual inspection of the contrasts at a liberal threshold ($P < 0.001$ uncorrected for multiple comparisons, spatial extent >4 voxels) revealed that multi-model problems resulted in small clusters of more activation in bilateral anterior cingulate gyrus, left middle frontal gyrus, and right insula and inferior parietal lobule. Small deactivations for multi-model as compared to single-model problems were found at this threshold in middle occipital gyrus, thalamus, head of caudate, and in the anterior lobe of the cerebellum. However, none of these clusters reached the threshold for statistical significance.

4. Discussion

The present study examined the neuro-cognitive processes underlying relational reasoning and the maintenance of the problem information in working memory. Neuronal activations *common* to both tasks were detected bilaterally in secondary visual cortices, medial parietal cortex, and medial anterior prefrontal cortex. Neuronal activations *distinct* for reasoning were found in right parahippocampal gyrus as well as in dorsal anterior cingulate cortex and bilateral dorsolateral prefrontal cortex. There was no reliable difference between determinate and indeterminate reasoning problems. During reasoning, the increase of activation in the precuneus covaried negatively with the participants' visuo-spatial skills. Finally, maintenance led to stronger activity than reasoning in superior and lateral parietal areas. In the following, we will discuss the implications of these findings for neuro-cognitive theories of reasoning and working memory.

4.1. Common activations in visual cortex

The most important finding was that in the absence of any task-correlated visual input, both reasoning and maintenance in working memory activated similar portions of the secondary visual cortices in both hemispheres, corresponding to V2 (Brodmann area 18; Fig. 3). This section of occipital cortex has consistently been found active when participants were required to visually imagine objects based on verbal descriptions or previous experience [5,23,36]. Lesions in this brain structure were found to have a devastating effect on the ability to form mental images [19]. The present results thus support the central assumption of mental model theory that people "naturally reason by imagining the state of the affairs described in the premises" ([11], p. 573).

Image 1:

Both reasoning and maintenance activate bilateral middle occipital gyrus

Image 2:

Reasoning activates right parahippocampal gyrus

Fig. 3. Occipital activation during both reasoning and maintenance, and parahippocampal activation during reasoning. Image 1 displays the rendering of the contrast [reasoning and maintenance] vs. rest, masked inclusively by the contrasts reasoning vs. rest and maintenance vs. rest. Image 2 displays the rendering of the contrast reasoning vs. rest. Renderings were thresholded for height at $Z = 3.09$, and for spatial extent at $P < 0.05$ corrected for multiple comparisons across the whole brain. Z-values were plotted onto saggital, coronal, and transverse sections of a standard template brain according to the colour scale given right of each transverse section. The crosshairs are positioned in the local peak voxel of the cluster. L: left hemisphere, R: right hemisphere, A: anterior end, P: posterior end.

This is in line with previous studies which found activity in parieto-occipital cortices during spatial-relational reasoning [25,33,37], and with the finding that dual-task disruption of visuo-spatial working memory results in an impairment of reasoning [31,35,71].

As a novel finding, the present study showed comparable occipital activation patterns for reasoning and for merely encoding and maintaining the problem information in working memory. Note that the maintenance task could have been solved by linguistic strategies, such as auditory rehearsal. However, we did not find activity in left-hemisphere neuronal systems devoted to language processing [64,65]. The activation of occipital cortex during both tasks thus appears related to the maintenance of visuo-spatially organized representations. This is congruent with the assumption that elementary cognitive operations may also be carried out with mental models [28].

However, it has to be stressed that the occipital activation found during reasoning and maintenance does not indicate that mental models are necessarily "visual" per se [28,33,37]. Generally speaking, a mental representation is referred to as a *visual image* if it is structurally similar to a real visual perception, i.e. if it is an integrated representation of the given information that represents colours, shapes, and metrical distances with a limited resolution, so that it can

be rotated and scanned [20,39–41]. Mental models, in contrast, also integrate different types of information, but they represent only information relevant to the inference and thus not necessarily visual details [28]. All sorts of information (even explicitly non-spatial types, such as kinship) may be included in mental models in an abstract spatial way, for example in a multi-dimensional array that only maintains ordinal and topological properties. It is for this reason that model-based reasoning interferes with other spatial tasks, but not necessarily with concurrent visual secondary tasks without a spatial component [35], and that irrelevant visual detail can even impede the process of reasoning [34]. We can thus assume that mental images are a subset of mental models [28], and that the models constructed by the participants in our study contained at least some visual details. This assumption is consistent with the introspection of our subjects, and it seems reasonable since visual features of the objects (i.e. their colour) were important for solving both types of problems.

4.2. Distinct activations for reasoning and maintenance

While the pattern of occipital activation is generally consistent with the theory of mental models, an open question is why the present study did not find parietal activation

during reasoning. The parietal cortex is normally thought to underlie reasoning based on mental models. It mediates the integration of sensory information into an egocentric (viewer-centered) spatial representation of the environment, and it is active during visual transformation tasks such as mental rotation [1,15,70,74]. In the present study, however, activity was observed in two brain structures associated with allocentric (object-centered) spatial processing: the right parahippocampal gyrus and the posterior cingulate cortex (Fig. 3). Lesions of both these structures lead to considerable deficits in memory for the spatial location of objects in humans and animals [45,47,58,66], and the right hippocampus has consistently been found active in neuroimaging studies examining imagined or online navigation through familiar environments [9,46,48]. The specific role of the right parahippocampal gyrus in this process has been identified as object-to-place encoding irrespective of the position of the viewer [46], while the posterior cingulate cortex is supposed to functionally link medial temporal regions (involved in spatial mapping of the environment) and parieto-occipital regions (involved in computing head-centered representations) in order to produce imaginable spatial representations of the environment in the precuneus [9,45].

Thus, one possible explanation for our findings is that allocentric spatial processes were engaged for the reasoning problems employed in the present study. In contrast to previous investigations [25,37], two-thirds of the present problems gave rise to multiple mental models. These presumably required the flexible assignment of spatial positions to the three objects until the conclusion was finally evaluated [29,30]. Note that the nature of a reasoning problem (determinate or indeterminate) was not evident until the second premise was fully processed. Subjects may thus have simply applied the economical strategy of uniformly constructing flexible *initial* or *preferred* mental models [30,32,60] for both types of reasoning problems. This account also offers an explanation why we did not detect differences in the neuronal processing of determinate and indeterminate reasoning problems. However, an alternative explanation is simply the lack of statistical power for such detailed comparisons, since our design mainly focused on the differences between all reasoning and working memory problems.

The finding that bilateral parietal activation was detected for the contrast of maintenance versus reasoning may also be explained by the representation likely used for this specific task. Unlike reasoning, maintenance did not require the flexible assignment of spatial positions to the objects, but rather the precise encoding of the objects and their spatial position. This may have been best accomplished by constructing a static visuo-spatial representation, in close resemblance to the visuo-spatial mental models employed during reasoning about determinate problems with fixed object–position relations. Maintaining such a representation presumably places a strong demand on the storage systems of spatial working memory, located in inferior and superior parietal cortices [51,59,64].

4.3. Covariation of activity with the participants' visuo-spatial skills

During reasoning, activation of a cluster located in the precuneus covaried negatively with an index of the participants' visuo-spatial skill (Fig. 2), while behavioural performance correlated positively with this index. In other words, the higher the participants' visuo-spatial skill, the better their reasoning performance, and the less activation present in the precuneus during reasoning. This pattern agrees with recent findings on the effects of skill level on neuronal activity [61]. In this study, participants solved sentence–picture verification problems with verbal or visuo-spatial strategies. Parietal activation during application of the visuo-spatial strategy correlated negatively with the participants' spatial skills, as predicted by a resource model of the underlying processes. The present results also support such an account; the reasoning problems seemed to have placed less demand on the visuo-spatial processing resources of participants with high skill levels, so that less activity in the relevant cortical regions was required. For the behavioural data alone, one may argue that this pattern mostly reflects the effect of general intelligence on both reasoning and Block Design Test performance. However, the correspondence of the behavioural and the neuroimaging data shows that specifically visuo-spatial resources are taxed by both tasks.

4.4. Prefrontal activations

Reasoning led to more activation than maintenance bilaterally in the dorsolateral prefrontal cortex (DLPFC; Fig. 4) and in the right dorsal anterior cingulate cortex (ACC), pointing to additional executive processes exclusively devoted to reasoning [6,10,12,17,63]. Which functions may these cortical areas subserve? One possibility is that the observed activations may simply reflect the increased difficulty of the reasoning problems, and thus the higher cognitive effort required for reasoning. This interpretation is suggested by studies on cognitive control, characterizing the role of the prefrontal-cingulate network as attentional control or performance monitoring in situations with a high possibility of committing errors [6,13,23,63]. However, effort-related activations in the ACC have been shown to be independent of more specific working memory processes located in the DLPFC [4]. Thus, processes related to heightened task difficulty do not fully account for the finding that both DLPFC and ACC showed heightened activation during reasoning.

Fletcher and Henson [21] state on the basis of a large number of previous working memory studies that "manipulation processes, operating on information already maintained in memory, engage DLFC" (p. 859), and Petrides [56] claims that this brain structure is typically involved "when several pieces of information in working memory need to be monitored and manipulated" (p. 85). Despite competing views [16,44,50], this process-specific hypothesis of DLPFC function is currently widely supported by a group of researchers

Image 1:

Reasoning vs. maintenance activates bilateral middle frontal gyrus

Image 2:

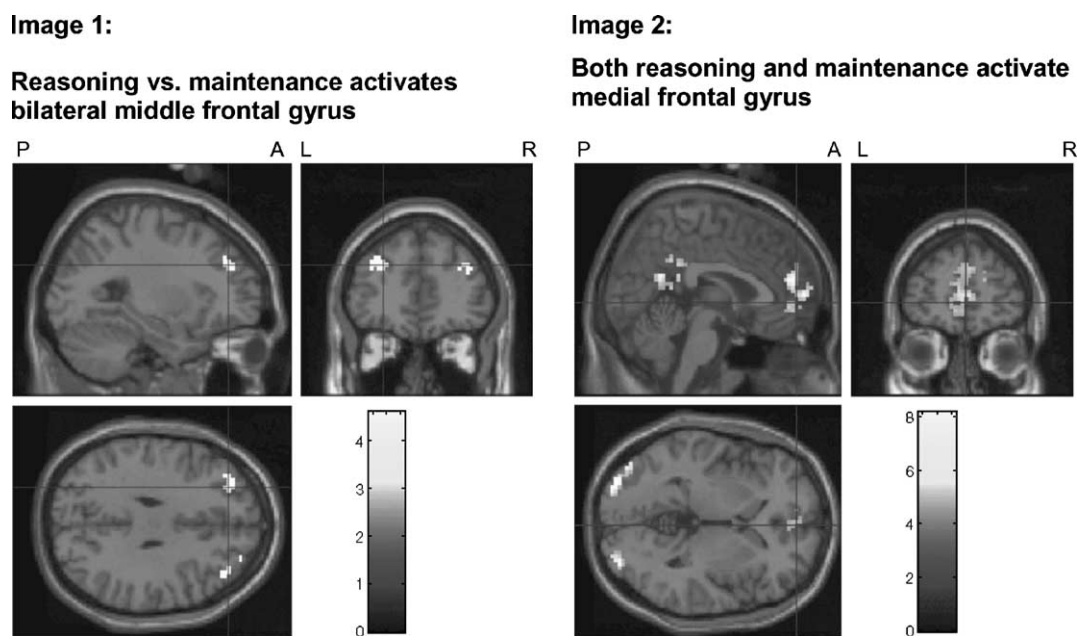**Both reasoning and maintenance activate medial frontal gyrus**

Fig. 4. Prefrontal activation during reasoning and maintenance. Image 1 displays the rendering of the contrast reasoning vs. maintenance. Image 2 displays the rendering of the contrast [reasoning and maintenance vs. rest], masked inclusively by the contrasts reasoning vs. rest and maintenance vs. rest. Renderings were thresholded for height at $Z = 3.09$, and for spatial extent at $P < 0.05$ corrected for multiple comparisons across the whole brain. Z-values were plotted onto saggital, coronal, and transverse sections of a standard template brain according to the colour scale given right of each transverse section. The crosshairs are positioned in the local peak voxel of the cluster. L: left hemisphere, R: right hemisphere, A: anterior end, P: posterior end.

[17,53,57]. The DLPFC activation found during reasoning may thus reflect the manipulation of the problem representation during the third stage of the reasoning process, when the initial mental model is actively varied in order to find counterexamples [27,28].

Alternatively, the DLPFC activation during reasoning may also reflect processes related to the integration of information from various sources [14,42]. Waltz et al. [73], for example, showed that patients with damage to the prefrontal cortex were strongly impaired on deductive and inductive reasoning tasks only when these required relational integration. Waltz et al. concluded that "postulating a neural system for integrating multiple relations provides an explanation of why a wide range of tasks, all of which depend on processing multiple relations simultaneously, are sensitive to prefrontal damage and activate DLPFC" (p. 124). Relational integration is an essential part of reasoning about the transitive inference problems employed in the present study, while it is not required for solving the maintenance problems. An interesting question for further studies is thus whether the engagement of the DLPFC during reasoning is related to the manipulation or the integration of information, and whether these processes are important during different stages of the reasoning process.

Apart from activations specific to reasoning, activations common to both reasoning and maintenance were also detected in medial portions of the anterior prefrontal cortex (APFC). A recent theoretical framework characterized the function of the APFC as the selection and coordination of (sub)goals, irrespective of the content of the material held and manipulated in working memory [21]. Support for this view is given by studies which found activity in lateral parts of this brain structure only when participants had to flexibly switch between multiple goals related to different tasks, but not during execution of either of the single tasks [8,38]. In the present study, the APFC activation may thus reflect a property of the experimental design, namely that participants had to select and apply the strategies for the two types of problems while holding in mind the overall goals of the experiment. By this account, and consistent with the results of the strategy interview, the more extensive APFC activation during maintenance may reflect the larger demand to develop an individual strategy for solving this problem type, while the cognitive strategy for reasoning may have been more pre-determined by the instructions.

5. Conclusions and open questions

The present study examined the neuronal processes devoted to reasoning and to the maintenance of the problem information in working memory. Both tasks engaged occipital cortex in the absence of correlated visual input. Reasoning was associated with stronger dorsolateral and medial prefrontal activation, whereas maintenance led to stronger lateral parietal activation. An index of the subjects' visuo-spatial abilities covaried negatively with activity of the precuneus during reasoning. In sum, these results support

the notion that relational reasoning is based on visuo-spatial mental models, and they help to distinguish the neuronal processes underlying reasoning and the maintenance of problem information in working memory.

The findings also raise a number of important questions: First, the cognitive operations described above should be active during different stages of the whole reasoning process. For instance, integration of information into a mental model should take place mostly during processing of the second premise. Event-related studies should thus directly examine the change in brain activity during various stages of reasoning. Second, our study leaves unresolved whether determinate and indeterminate problems lead to differences in cortical activity during reasoning. Third, it remains to be determined to what degree visuo-spatial processes also underlie other forms of reasoning that do not explicitly require visualization.

Acknowledgements

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