fMRI Evidence for a Three-Stage Model of Deductive Reasoning

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Abstract

■ Deductive reasoning is fundamental to science, human culture, and the solution of problems in daily life. It starts with premises and yields a logically necessary conclusion that is not explicit in the premises. Here we investigated the neurocognitive processes underlying logical thinking with event-related functional magnetic resonance imaging. We specifically focused on three temporally separable phases: (1) the premise processing phase, (2) the premise integration phase, and (3) the vali- dation phase in which reasoners decide whether a conclusion logically follows from the premises. We found distinct patterns of cortical activity during these phases, with initial temporo- occipital activation shifting to the prefrontal cortex and then to the parietal cortex during the reasoning process. Activity in these latter regions was specific to reasoning, as it was signifi- cantly decreased during matched working memory problems with identical premises and equal working memory load. ■

INTRODUCTION

How do humans think deductively? Why do we commit mistakes in reasoning? And which patterns of brain activity might underlie deductive reasoning? Cognitive science has focused on the first two questions and provided some tentative answers. It is believed that we think deductively by applying different mental algo- rithms, partially by constructing models in the usual logical sense and partially by applying mental rules, which are similar to rules in computer programs. It is also believed that humans have the competence to per- form error-free deductive inferences. Errors do occur, however, because reasoning performance is limited by the capacities of the cognitive system, misunderstand- ing of the premises, ambiguity of problems, and moti- vational factors (Manktelow, 1999; Evans, Newstead, & Byrne, 1993; Johnson-Laird & Byrne, 1991).

But how do our brains enable us to solve deductive reasoning problems? This question is much less well understood. Recent functional brain imaging studies have provided some of the first insights into the brain circuits underlying deductive reasoning. Reasoning with abstract premises seems to involve the right hemi- sphere, whereas reasoning with concrete material relies on processing in the left hemisphere (Goel & Dolan, 2001; Goel, Buchel, Frith, & Dolan, 2000). During reason- ing, portions of the parieto-occipital cortices are active,

pointing to the role of visuospatial processes (Knauff, Ruff, & Johnson-Laird, 2003; Ruff, Knauff, Fangmeier, & Spreer, 2003; Knauff, Mulack, Kassubek, Salih, & Greenlee, 2002). The more visual features are described in the reasoning problem, the more activity in occipital cortical areas can be found (Knauff, Fangmeier, et al., 2003). Moreover, reasoning-related activity in parietal areas correlates with visuospatial ability (Ruff, Knauff, Fangmeier, & Spreer, 2003).

However, most of these studies have one pitfall in common. They presented the problems as sentences, ei- ther on the screen or via headphones. Hence, reasoning- related brain activity may have been confounded by higher-level linguistic processing. In addition, many of these studies examined the brain activation during the whole reasoning process in a blocked fashion, and thus, could not distinguish reasoning-related processes during different stages of problem processing. A few studies so far compared the neuronal processes during the important conclusion sentence of the reasoning problem with the presentation of irrelevant control sentences (e.g., Goel & Dolan, 2001). However, these control sen- tences clearly did not need to be processed as elaborately as the reasoning problem, and did not provide any information about brain processes during premise pro- cessing. Thus, it is unclear whether reasoning is associ- ated with distinct subprocesses not related to sentence processing, and how these processes may be differen- tially involved in different stages of reasoning.

The aim of the present study was to disentangle the neurocognitive subprocesses underlying the different phases in the reasoning process, and at the same time

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to overcome the potential linguistic confound in the previous studies on the neuronal basis of deductive reasoning. We employed event-related functional magnetic resonance imaging (fMRI) with 12 participants, who solved 32 linear syllogisms with a spatial content (while in the scanner). We decided to use problems with a spatial content, because spatial relations are easily understood by logically untrained participants. Because we aimed at distinguishing the pure reasoning process from the maintenance of information in working memory, in a second condition participants had to simply keep the premises of the identical problems in working memory (maintenance problems) without making inferences (explanation below). It is important to note that the premises and the conclusion of the inference problems were each presented as single display frames, by replacing the sentential premises with graphic arrangements describing the spatial relations between three letters. With this procedure, no further linguistic processing was necessary to extract the spatial relations between the objects. Moreover, the processing of the first premise, the second premise, and the conclusion was time-locked to the brief presentation of the letter arrangements (Figure 1). Thus, we could examine the brain activity elicited by the different phases of the reasoning process.

Based on behavioral findings concerning the cognitive processes involved in reasoning (Rader & Sloutsky, 2002; Evans et al., 1993; Johnson-Laird & Byrne, 1991), we predicted that there should be distinct patterns of neuronal activation associated with the *three* phases of the reasoning process: During the presentation of both the first and second premises, reasoners have to process and keep in mind the two letters of each premise and their spatial relation (*premise processing phase*). During the second premise exclusively, the two premises are integrated into one unified representation and a putative conclusion is drawn (*premise integration phase*).

Finally, reasoners compare the conclusion they drew from the premises with the displayed conclusion, and indicate by pressing a button whether the displayed conclusion is ''True'' or ''False.'' We denote this as the *validation phase*. It is critical to appreciate that the processing of the matched maintenance problems also proceeded in three phases, but that there was no need for premise integration during the second stage. Moreover, in the third stage of the maintenance problems, participants only had to remember the temporal sequence in the premises and to match it with the third sentence presented. They did not draw inferences, but the memory load was the same as in the reasoning problems. Although the different presentations thus cannot be called ''premises'' in the literal sense, we henceforth use the terms to clarify the correspondence to the reasoning problems. On any given trial, a letter displayed prior to problem presentation identified the following problem as a reasoning or a maintenance problem. We hypothesized that the reasoning and the maintenance problems should both entail the maintenance of premises, but that only the reasoning problems should demand for the integration of the premises and the validation of a putative conclusion. To explore the influence of individual differences in visuospatial skills on brain activity during the reasoning and maintenance problems, the participants were tested after the experiment with the ''Block Design Test'' (BDT) of the German Equivalent to the Wechsler Adult Intelligence Scale (HAWIE-R, Tewes, 1991).

RESULTS

Behavioral Data and Post-test

As expected, the behavioral data collected inside the scanner showed that reasoning problems were significantly more difficult than maintenance problems (Evans
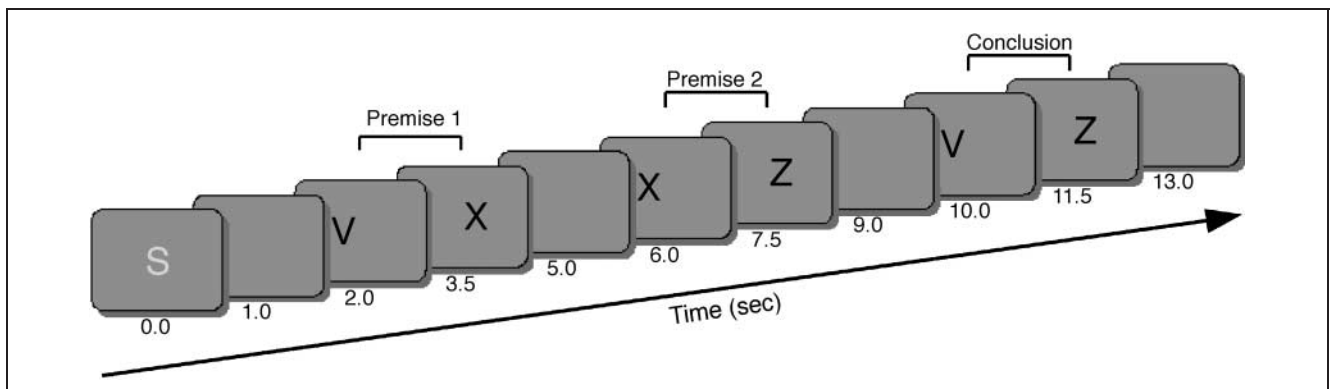

Figure 1. Sequence of a reasoning problem. Prior to each problem, an ''S'' (''**S**chließen'' in German) or an ''E'' (''**E**rinnern'' in German) was presented for 1 sec. The spatial relation between the two letters of each premise or conclusion was coded by placing it right or left from the midpoint of the screen. Each trial began with presentation of the first letter for 1500 msec, followed by the second letter for 1500 msec, and a pause for 1000 (first premise), making a total of 4 sec. The period for the second premise and the conclusion or maintenance was the same as during the first premise.

et al., 1993; Johnson-Laird & Byrne, 1991) in terms of accuracy (91% < 97% correct answers; $Z = 2.31$, $p = .021$) and latency (3021 msec > 2843 msec response time; $Z = -2.04$, $p = .041$, Wilcoxon Test because of non-normal distributions, see Siegel & Castellan, 1989).

The spatial-constructive intelligence scores (BDT) of all participants (measured after scanning) were within the normal to superior range (mean value equivalent to an IQ of 116, standard deviation equivalent to 15 IQ-points, lowest value equivalent to an IQ of 105).

fMRI Data

Whole-Brain Analysis

For the *reasoning problems*, the brain imaging data showed clearly distinguishable brain activation patterns during the different phases of the inference process (Table 1 and Figure 2A–C). First, the *premise processing phase* activated two large bilateral regions in the occipito-temporal cortex (OTC; Figure 2A). Second, during the *premise integration phase* (Figure 2B), these two regions in the OTC and an additional region in the anterior prefrontal cortex (APFC) were activated. The cluster in the APFC covered parts of the middle frontal (Brodmann's area [BA] 10) and the anterior cingulate (BA 32). Third, the *validation phase* activated three regions: two in the prefrontal cortex (PFC) and one in the posterior parietal cortex (PPC; Figure 2C). More precisely, the clusters in the PFC were located in the middle frontal gyrus (BA 9, 8, and 6), in the right hemisphere extending into the medial frontal and the anterior cingulate (BA 32). The PPC activation covered parts of the precuneus (BA 7), and of the superior and inferior parietal lobule (BA 7, 40) in both hemispheres.

The contrasts for the *maintenance problems* were calculated in a similar fashion as those for reasoning (see Methods). During the *premise processing phase*, we found similar OTC activations as those obtained during reasoning (compare Figure 2A vs. Figure 2D and Table 2). During presentation of the second premise (*premise maintenance phase*), which now required only premise maintenance but not integration, we again found activation in the OTC, APFC, and PPC; however, activity in the APFC and the PPC was significantly lower than during reasoning (see below, and compare Figure 2B vs. 2E, Figure 2C vs. 2F, Figure 2G vs. 2H. Significant differences between reasoning and maintenance problems are shown in the bar charts in Figure 4 and in Table 3).

We also examined the overlap between the reasoning- and maintenance-related activities in a conjunction analysis (displayed in Figure 3A–C). Congruent with the visual inspection of the activity during the different problems, activity *common* to both problems was found in the OTC for the first and second phases (inferior and middle occipital gyrus, middle temporal cortex (TC), lingual gyrus, fusiform gyrus, BA 18, 19, 37), and in the

PPC (inferior and superior parietal lobule and precuneus BA 40, 7) for the third phase.

When directly comparing the activations elicited by reasoning and maintenance (Figure 4A–C and D–F), five regions showed higher activation during reasoning than during maintenance: the APFC (BA 10) and the basal ganglia during the second phase (Figure 4B), and the PFC (left/right: middle and medial frontal cortex, BA 8, 6, 32) and right PPC (precuneus, BA 7) during the third phase (Figure 4C). Note that the conjunction analysis pointed out that bilateral PPC activity is common for both problems, however, only activity in the right pre-cuneus (BA 7) was significantly higher during the third phase of reasoning than during the corresponding stage of maintenance. Conversely, only two regions in the left TC (TC L, middle and superior temporal gyrus, BA 21, 22) during the premise processing phase (Figure 4D) and one region in the medial occipital cortex (OC M, cuneus, BA 18) during the maintenance validation phase (Figure 4F) showed significantly higher activity during maintenance than during reasoning. A region-of-interest (ROI) analysis of the mean activity in the eight regions found in the whole-brain analysis was made. The signals from each cluster were directly compared with separate 2×3 factorial analyses of variance (ANOVAs, Problem $\times$ Phase, repeated measurements) in which all interactions were significant (significant differences tested with a t test for paired samples between the problems in each phase were marked with an asterisk in the bar charts in Figure 4). Three additional significant differences were found in the ROI analysis in the right APFC during the maintenance validation phase and in the medial and lateral TC during the reasoning validation phase (see Figure 4 bar charts).

Reasoning Difficulty

During performing working memory problems, the participants showed higher accuracy and faster response times than during reasoning problems. One possible explanation for the differences between reasoning and maintenance problems thus could be these differences in performance difficulty. To rule out this explanation, we calculated an additional model for each participant, in which we included a regressor which estimated, across trials, the parametric modulation of neuronal response by trial response time. The regressor partialed out the effect of trial difficulty of every contrast between reasoning and maintenance. Nevertheless, we found the same significant differences between the conditions in the APFC during the second phase, and for the left/right PFC and the right PPC during the third phase.

Individual Differences in Brain Activity

To examine possible relations between individual spatial ability and reasoning-related neocortical brain activity,

Table 1. Localization of Activation during the Reasoning Problems

Anatomical Region	BA	t Score	Talairach Coordinates		
			x	y	z
Premise Processing Phase					
Cluster left occipito-temporal (VOX = 493***)					
Middle occipital gyrus (L)	37	12.79	−48	−70	4
Inferior occipital gyrus (L)	19	10.49	−44	−70	−3
Middle occipital gyrus (L)	19	9.64	−32	−85	15
Cluster right occipito-temporal (VOX = 428***)					
Inferior occipital gyrus (R)	18	11.25	44	−74	0
Middle occipital gyrus (R)	37	11.07	44	−66	3
Superior temporal gyrus (R)	39	9.54	48	−54	10
Premise Integration Phase					
Cluster anterior medial frontal (VOX = 110***)					
Anterior cingulate (R)	32	5.67	20	39	2
Medial frontal gyrus (R)	10	5.39	16	50	−3
Anterior cingulate (L)	32	4.98	−20	39	2
Cluster left occipito-temporal (VOX = 269***)					
Fusiform gyrus (L)	37	9.43	−32	−59	−7
Fusiform gyrus (L)	20	7.32	−28	−40	−18
Parahippocampal gyrus (L)	36	6.93	−20	−36	−12
Cluster right occipito-temporal (VOX = 216***)					
Fusiform gyrus (R)	19	6.70	32	−66	−7
Cerebellum, Culmen (R)	—	5.94	32	−55	−21
Cuneus (R)	18	5.72	16	−93	8
Reasoning Validation Phase					
Cluster medial and right frontal (VOX = 140***)					
Medial frontal gyrus (L)	32	6.38	−8	10	47
Middle frontal gyrus (R)	6	6.22	28	−1	52
Middle frontal gyrus (R)	6	5.62	36	−5	52

Table 1. (*continued*)

Anatomical Region	BA	t Score	Talairach Coordinates		
			x	y	z
Cluster left frontal (VOX = 47**)					
Middle frontal gyrus (L)	6	7.57	−36	2	48
Middle frontal gyrus (L)	9	3.46	−52	10	36
Precentral gyrus (L)	6	3.37	−32	−9	52
Cluster bilateral parietal (VOX = 388**)					
Inferior parietal lobule (L)	40	7.27	−44	−44	46
Inferior parietal lobule (L)	40	6.75	−32	−45	43
Precuneus (R)	7	5.89	24	−68	40

RFX Analysis: SPM(*t*)s were thresholded for height at *t* = 3.0, and cluster level *p* ≤ .05, corrected for multiple comparisons. Locations, *t* scores, and Talairach coordinates refer to the peak voxels of the cluster. The correspondence of this voxel to Brodmann's areas is only established when applicable; however, note that localization can only be performed at the level of the whole cluster. VOX = number of voxels; L = left; R = right.

**$p \leq$ .01.

***$p \leq$ .001.

we examined the correlation (in a different model in SPM99) between the performance on the BDT and the neural activation in each phase of the two problems (Ruff et al., 2003). In this analysis, we found statistically significant negative correlations of the participants' BDT score with neural activity during the reasoning premise *integration phase* in the left and right PPC but not during maintenance. These correlations, along with other correlations, are summarized in Table 4.

DISCUSSION

The most fundamental result of our study is that different cortical structures are activated during different phases of logical thinking. Activation of occipito-temporal structures was found in the *premise processing phase*, activation in the APFC in the subsequent *integration phase*, and activation of the PPC and PFC during the final *reasoning validation phase*. Because problems were presented as graphic depictions of the state of the affairs, these activations cannot be explained by reading and linguistic processing of the premises. Moreover, the maintenance condition employed in the present study was identical to the reasoning problems in terms of problem content, visual display, and working memory load. In this condition, we found significant lower APFC, PFC, and right PPC activations in the *premise maintenance phase*, and in the *maintenance validation phase*, respectively.
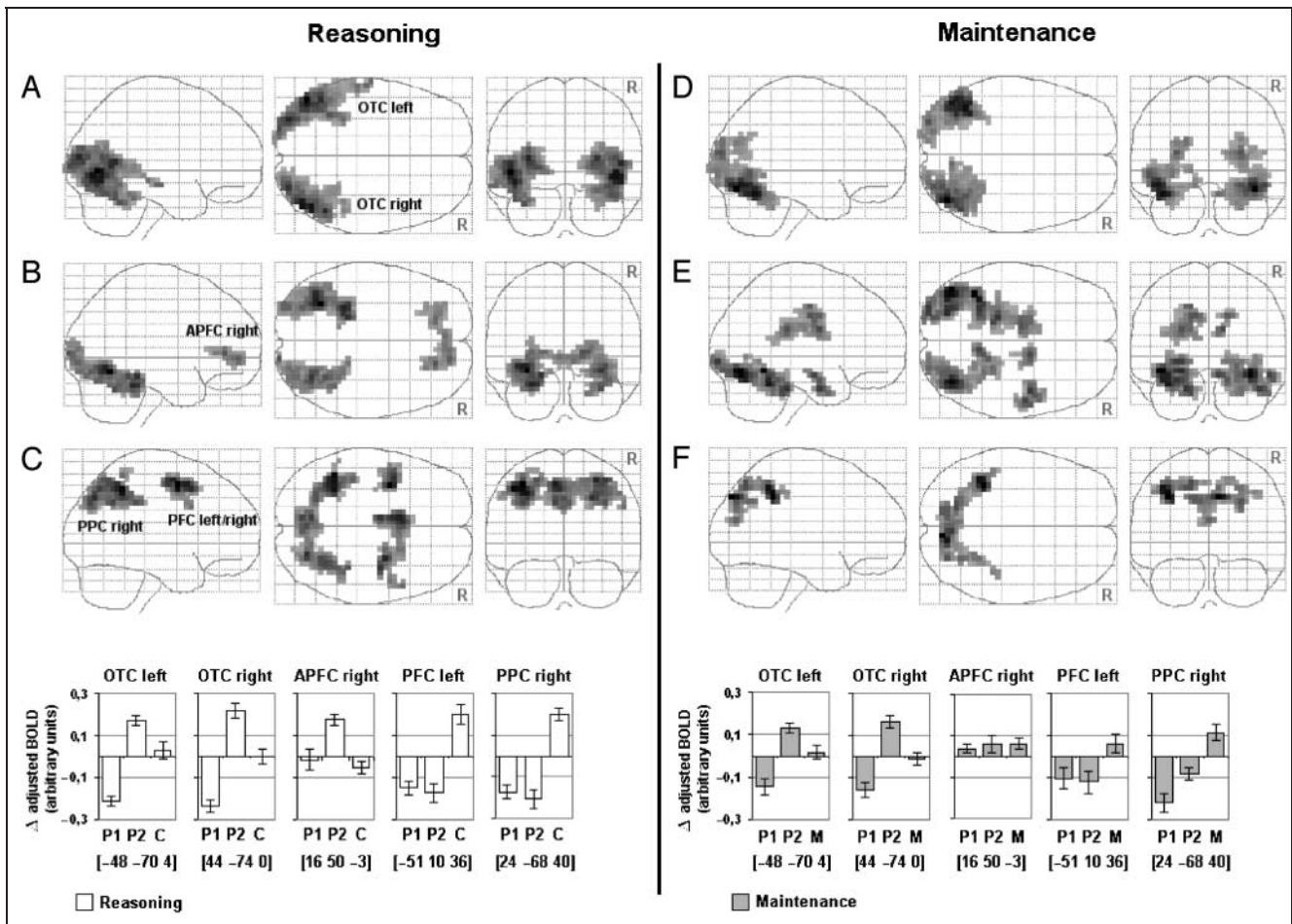
Figure 2. Brain activation during reasoning and maintenance. Activated regions are shown separately for reasoning and maintenance during the three phases. *Reasoning problems:* (A) premise processing phase, (B) integration phase, (C) validation phase. *Maintenance problems:* (D) premise processing phase, (E) premise maintenance phase, (F) validation phase. The activations were significant at the cluster level calculated with SPM99 ($p \leq .05$, corrected, threshold $t = 3.0$). The bar charts with mean error bars below display the beta means for each phase (± 12 mm around the peak voxel within the cluster): first phase (P1), second phase (P2), and the validation phase for the conclusion (C) or for maintenance (M). The position of the peak voxel is shown by the Talairach coordinates (TAL [$X Y Z$]) below each bar chart.

Another finding is that during reasoning, the increase of activation in the PPC and right frontal cortex covaried negatively with the participants' visuospatial skills. In the following, we will discuss these findings in the framework of a neurocognitive three-stage model of human (relational) reasoning.

Premise Processing Phase

The *initial phase*, the processing of the two premises, activated bilateral cortical structures in the OTC. These areas have been found active during problems such as visual working memory and imagery (Kosslyn, Ganis, & Thompson, 2001; Postle, Stern, Rosen, & Corkin, 2000; Toga & Mazziotta, 2000; Courtney, Ungerleider, Keil, & Haxby, 1996; Kosslyn, et al., 1994), and correspond to the ventral "what"-stream (Ungerleider, Courtney, & Haxby, 1998). The activity found in our study is consistent with the notion that reasoners use their general knowledge to represent in "small scale" what the prem-

ises describe. Such models are often described as a type of diagram because their structure is analogous to the structure of the state of affairs that they stand for. The activity also agrees with the finding that reasoning with materials that are easy to visualize leads to activity in the visual association cortex (Knauff, Fangmeier, et al., 2003; Ruff et al., 2003; Knauff et al., 2002; Goel et al., 2000). However, a novel finding in our study is that these visual processes seem to be engaged mostly during the first and second phases of the reasoning process. In addition, they were similarly elicited by both the reasoning and the maintenance problems (see Figure 3A and B). This demonstrates that the premises are at first processed in a similar fashion under both conditions, and that the participants maintained the premises in working memory by visual strategies, not exclusively by verbal rehearsal (Smith & Jonides, 1998; Smith, Jonides, Marshuetz, & Koeppe, 1998) or language-based representations postulated by the formal rules theory (Braine & O'Brien, 1998; Rips, 1994).

Table 2. Localization of Activation during the Maintenance Problems

Anatomical Region	BA	t Score	Talairach Coordinates		
			x	*y*	*z*
Premise Processing Phase					
Cluster left occipito-temporal (VOX = 295***)					
Fusiform gyrus (L)	37	11.43	−40	−59	−14
Inferior occipital gyrus (L)	19	10.92	−44	−70	−7
Middle occipital gyrus (L)	19	7.09	−28	−88	19
Cluster right occipito-temporal (VOX = 311***)					
Fusiform gyrus (R)	19	12.96	40	−74	−10
Middle occipital gyrus (R)	37	8.09	48	−63	−7
Fusiform gyrus (R)	37	7.34	36	−59	−11
Premise Maintenance Phase					
Cluster left Insula (VOX = 161***)					
Insula (L)	13	5.84	−24	−30	24
Cingulate gyrus (L)	24	5.70	−12	−10	34
Cingulate gyrus (L)	24	5.51	−16	−10	41
Cluster right temporal (VOX = 57**)					
Fusiform gyrus (R)	20	6.64	44	−5	−23
Middle temporal gyrus (R)	21	6.26	52	−8	−13
Middle temporal gyrus (R)	21	5.07	52	3	−27
Cluster left occipito-temporal (VOX = 285***)					
Inferior occipital gyrus (L)	19	9.50	−44	−70	−7
Fusiform gyrus (L)	37	9.18	−40	−51	−8
Fusiform gyrus (L)	37	8.05	−36	−48	−18
Cluster right occipito-temporal (VOX = 228***)					
Fusiform gyrus (R)	19	9.11	36	−70	−10
Cerebellum, Culmen (R)	—	6.20	8	−47	−11
Parahippocampal gyrus (R)	36	5.45	16	−40	−15
Maintenance Validation Phase					
Cluster left parietal (VOX = 90***)					
Supramarginal gyrus (L)	40	7.73	−36	−41	39
Inferior parietal lobule (L)	40	6.94	−40	−44	46

Table 2. (*continued*)

Anatomical Region	BA	t Score	Talairach Coordinates		
			x	*y*	*z*
Precuneus (L)	7	5.18	−16	−64	51
Cluster right parietal (VOX = 154**)					
Precuneus (R)	7	7.67	8	−76	41
Precuneus (R)	7	5.64	4	−68	40
Precuneus (R)	19	4.97	28	−72	37

RFX Analysis: SPM(t)s were thresholded for height at $t = 3.0$ and cluster level $p \leq .05$, corrected for multiple comparisons. Locations, t scores, and Talairach coordinates refer to the peak voxels of the cluster. The correspondence of this voxel to Brodmann's areas is only established when applicable; however, note that localization can only be performed at the level of the whole cluster. VOX = number of voxels; L = left; R = right.

**p ≤ .01.

***p ≤ .001.

However, the maintenance processing phase additionally activated the left TC (medial and superior temporal gyrus, BA 21, 22; see Figure 4D). This might indicate the additional demand of the maintenance problem to remember both premises and their presentation sequence as separate entities. During the reasoning problems the premises might be integrated into one single representation, which might be less demanding to maintain (see below).

Integration Phase

The *second stage* of the reasoning problem comprised the integration of the information from the first and second premises. Behavioral data indicate that such integration of premise information occurs during processing of the second premise (Maybery, Bain, & Halford, 1986). In this phase, the reasoners construct a *single* integrated model of the state of affairs described in the premises, so that the premises of the reasoning problem are no longer represented as separate entities in working memory (Mani & Johnson-Laird, 1982).

We found significantly higher activation in the APFC (see Figures 2B and 4B) during the integration phase. This activation is most likely to reflect a process specific to reasoning, such as premise integration. This is consistent with other studies that have found the APFC to be involved in relational integration during reasoning, or in *considering multiple relations simultaneously* (Christoff et al., 2001; Prabhakaran, Rypma, & Gabrieli, 2001; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000; Waltz et al., 1999). Further support for a role of the APFC in premise integration comes from a study by Kroger et al. (2002), who found that APFC activity corresponded to the relational complexity of a problem, and not to

Table 3. Localization of Activation between Reasoning and Maintenance

Anatomical Region	BA	t Score	Talairach Coordinates x	y	z
Premise Processing Phase (Phase 1)					
Reasoning minus Maintenance	no additional activity measured				
Maintenance minus Reasoning					
TC L lateral (VOX = 14***)					
Middle temporal gyrus (L)	21	4.31	−59	−46	6
TC L medial (VOX = 17***)					
Superior temporal gyrus (L)	22	4.17	−44	−39	2
Middle temporal gyrus (L)	21	3.63	−48	−47	2
Integration Phase (Phase 2)					
Reasoning minus Maintenance					
APFC R (VOX =10***)					
Medial frontal gyrus (R)	10	3.74	12	50	−3
Basal ganglia (VOX = 18***)					
Claustrum (R)	—	4.18	24	27	−1
Putamen (R)	—	3.80	20	16	7
Caudate body (R)	—	3.65	20	24	10
Maintenance minus Reasoning	no additional activity measured				
Maintenance/Reasoning Validation Phase (Phase 3)					
Reasoning minus Maintenance					
PFC L (VOX = 42***)					
Superior frontal gyrus (L)	8	4.60	−20	18	43
Middle frontal gyrus (L)	6	3.82	−36	6	48
Middle frontal gyrus (L)	6	3.58	−40	14	44
PFC R (VOX = 76***)					
Medial frontal gyrus (R)	32	6.93	20	10	47
Middle frontal gyrus (R)	8	6.27	24	18	40
Middle frontal gyrus (R)	6	3.36	36	6	44

Table 3. (continued)

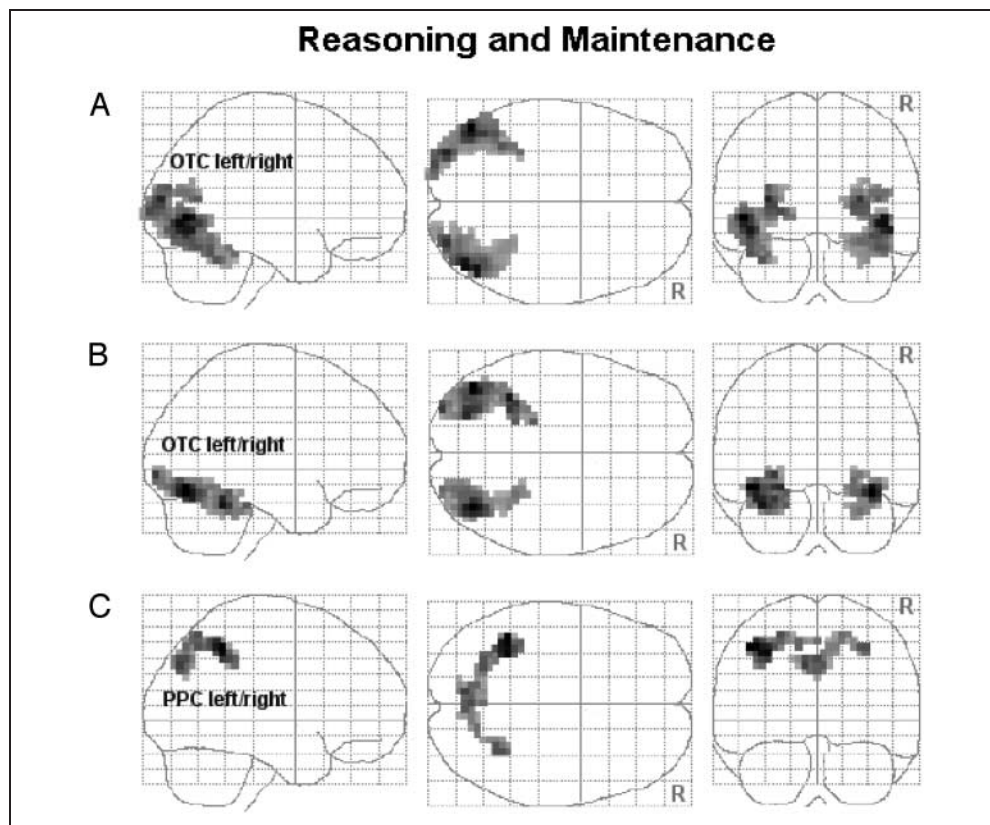| Anatomical Region	BA	t Score	Talairach Coordinates x	y	z
PPC R (VOX = 33***)					
Precuneus (R)	7	4.81	12	−59	58
Precuneus (R)	7	4.10	24	−60	51
Maintenance minus Reasoning					
OC M (VOX = 26***)					
Cuneus (R)	18	4.83	12	−77	22
Cuneus (M)	18	3.54	0	−80	26
Cuneus (L)	18	3.33	−12	−76	26

SPM(t)s were thresholded for height at t = 3.0. Locations, t scores, and Talairach coordinates refer to the peak voxels of the cluster. The correspondence of this voxel to Brodmann's areas is only established when applicable. We calculated separate 2 × 3 factorial ANOVA (repeated measurements) for all obtained regions (all interactions were significant at p ≤ .01, df = 2, 22) and a paired-samples t test compared the relevant factor levels. VOX = number of voxels; L = left; R = right; M = medial.

***p ≤ .001, df = 11.

general problem difficulty. Finally, a review of the function of an APFC structure (anterior part of BA 10) suggests that this area is responsible for relational integration, and the more general combination and coordination of outputs from multiple cognitive operations (Ramnani & Owen, 2004). Note that such integration processes were not necessary during pure maintenance problems, for which we found significant lower APFC activation in the corresponding phase.

One might object that several alternative explanations for these results can be derived from the working memory literature, which have linked activity in the APFC during higher cognitive problems with working memory storage capacity (Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999), verbal memory encoding (Rypma & D'Esposito, 1999), the generation and evaluation of hypotheses (Goel & Vartanian, 2005), or other working memory subprocesses (Goel, Shuren, Sheesley, & Grafman, 2004; Prabhakaran, Rypma, et al., 2001; Deglin & Kinsbourne, 1996; Gabrieli, Singh, Stebbins, & Goetz, 1996; Kyllonen & Christal, 1990; Salthouse, Mitchell, Skovronek, & Babcock, 1989). Moreover, several reviews and meta-analyses found a substantial overlap of prefrontal activity patterns across different cognitive problems, possibly pointing to more generic processes than premise integration (Wager & Smith, 2003; Duncan & Owen, 2000). However, such working-memory-based explanations for the APFC activations during the second phase of our reasoning problems seem unlikely, as the memory load for both reasoning and maintenance problems was identical. In addition,

Figure 3. Common brain activation. Common activated regions for both problems were shown in the glass brain. (A) Reasoning and maintenance first phase; (B) Reasoning and maintenance second phase; and (C) Reasoning and maintenance third phase. All activations were significant at the cluster level calculated with SPM99 ($p \leq .05$, corrected, threshold $t = 3.0$).

we controlled the difficulty differences between the two problems with two strategies: Only correctly solved problems were used for our results, and partialing out the discrepancies in difficulty for any given trial (via parametric modulation of BOLD responses by trial response time) did not change our results.

Validation Phase

In the *final phase*, in which a putative conclusion must be verified, we found activations in the bilateral PPC and the PFC, which were more marked for the reasoning than for the maintenance problems (Figure 4 bar charts). The PPC plays an important role in spatial processing and working memory (Burgess, Maguire, Spiers, & O'Keefe, 2001; Oliveri et al., 2001; Postle, Berger, & D'Esposito, 1999; Smith et al., 1998; Baker, Frith, Frackowiak, & Dolan, 1996) and in the integration of sensory information from all modalities into egocentric spatial representations (Xing & Andersen, 2000; Bushara et al., 1999; Andersen, Snyder, Bradley, & Xing, 1997; Colby & Duhamel, 1996).

Our finding thus highlights the critical role of modality-independent spatial representations specifically during the *validation* of the premises. Note that this account also resolves inconsistencies in previous neuroimaging studies on reasoning. These studies have similarly implied that the parietal cortex may play a key role in reasoning based on mental models, which are sup-

posed to be of abstract spatial nature. However, these studies have also shown concurrent activation of visual association cortices (Goel & Dolan, 2001; Goel et al., 2000), which points to the role of visual mental imagery in reasoning (Knauff, Fangmeier, et al., 2003; Ruff et al., 2003). The present study unifies these accounts, because it shows for the first time that visual association areas are indeed involved in premise processing and the construction of an initial static representation of the initial model, but that more abstract spatial representations held in parietal cortices are important for subsequent processes, in particular, when the model must be verified. Our data also underline that such reasoning-specific processes in the parietal cortex might be lateralized to the right hemisphere. Although bilateral parietal structures were commonly activated by both the reasoning and the maintenance problems (Figure 3C), consistent with the proposed involvement of the parietal cortex in elementary working memory processes (Wager & Smith, 2003), we found the right precuneus to be significantly more active during reasoning validation than during the corresponding phase of the maintenance problems (Figure 4C). The additional activation of prefrontal structures during this phase (BA 8, 6, and dorsal anterior cingulate cortex) indicates that further executive processes may be necessary for the control of this validation phase (Fletcher & Henson, 2001; Smith & Jonides, 1999). The main activity in the PFC lies in the middle frontal gyrus (BA 6, 8), bilaterally and covers parts of the
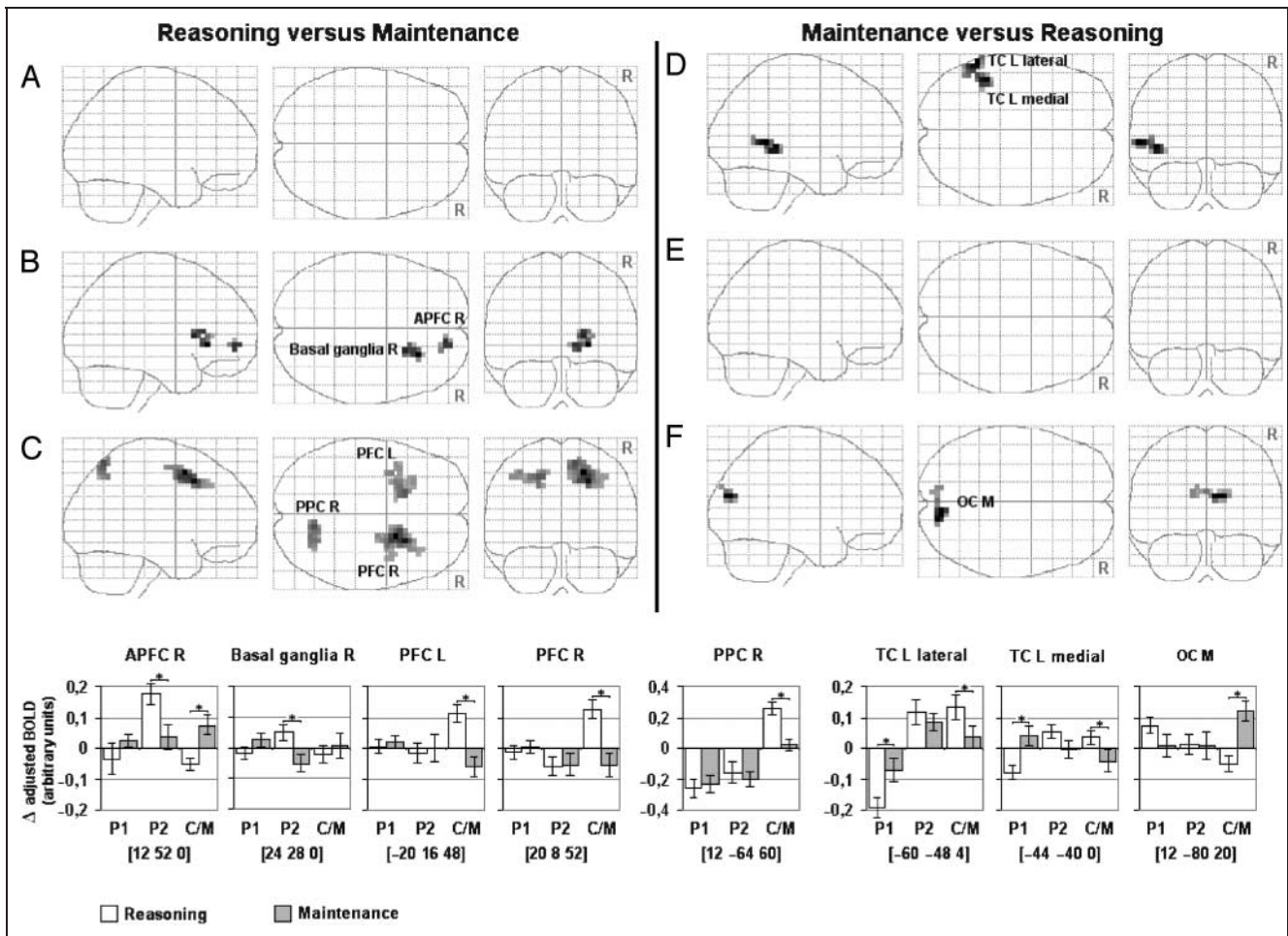
Figure 4. Brain activation between conditions. The figure shows all differences in activation between reasoning and maintenance. Reasoning versus maintenance: (A) first phase, (B) second phase, and (C) third phase. Conversely, contrasts for the first, second, and third phases are displayed at (D), (E), and (F), respectively. The first phase corresponds to the premise processing phase, the second phase to the reasoning integration and premise maintenance phase, and the third phase to the reasoning or maintenance validation phase. All highest peak voxels of a cluster were significant at the voxel level calculated with SPM99 (threshold $t = 3.0$). *ROI analysis:* The bar charts with mean error bars below display the beta means for each phase: first premise (P1), second premise (P2), and the validation for the conclusion (C) or for maintenance (M). Significant differences (paired t test, $p \leq .05$) between the problems within a phase are labeled with asterisks. The position of the peak voxel is shown by the Talairach coordinates (TAL [$X\,Y\,Z$]) below each bar chart.

caudal superior frontal sulcus. Anatomical data show that the posterior dorsolateral PFC BA 8 and rostral BA 6 have bidirectional connections with the PPC, for example, BA 7 and the more rostral-lying DLPFC (Petrides & Pandya, 1999). We assume that this activation has to do with the variation of the model to check putative conclusions (Johnson-Laird & Byrne, 1991) that was not necessary for maintenance problems. This assumption is also supported by the findings from Ruff et al. (2003). In this study, we used indeterminate problems (i.e., problems in which multiple solutions must be considered). Such problems require extensive model variation and we found increased activation in the rostral DLPFC, corresponding to BA 9. However, the study by Ruff et al. differs in many other respects from the present study and the block design only showed an activation mix of all reasoning stages. Further studies are needed to explore the role of specific areas in the

DLPFC if reasoners solve problems that require extensive model variation.

Individual Differences

In a previous study, we found a negative correlation between reasoning-related activity in the right parietal cortex and individual spatial ability (Ruff, Knauff, & Fangmeier, 2004; Ruff et al., 2003). We explained that finding by a resource-model, in which the reasoning problems seemed to have placed less demand on visuo-spatial processing resources of participants with high skill levels, so that less activity in the relevant cortical regions was required (Ruff et al., 2003, see also Keller, Carpenter, & Just, 2001; Just, Carpenter, Keller, Eddy, & Thulborn, 1996). Here, we replicated this finding, but can extend the explanation with respect to the specific stage of the reasoning process that showed this rela-

Table 4. Correlation between Individual Skill Differences and BOLD Signal during the Problems

Anatomical Region	BA	t Score	Talairach Coordinates x	y	z
Reasoning					
Premise Processing Phase					
		No significant cluster			
Premise Integration Phase					
PPC L (NC, VOX = 115***)					
Precuneus	7	5.79	−20	−60	47
Cingulate gyrus	31	5.28	−20	−53	32
Precuneus	7	4.19	−24	−76	41
PPC R (NC, VOX = 106***)					
Cingulate gyrus	31	5.22	20	−46	21
Superior parietal lobule	7	5.07	28	−64	40
Basal ganglia	—	5.07	28	−34	13
FC R (NC, VOX = 85***)					
Medial frontal gyrus	6	5.36	4	−24	57
Precentral gyrus	4	5.26	16	−20	56
Precentral gyrus	4	4.78	32	−17	52
Validation Phase					
Basal ganglia/Thalamus L (NC, VOX =48*)					
Basal ganglia	—	4.56	−16	1	15
Thalamus	—	4.52	−16	−23	16
Thalamus	—	4.43	−8	−3	11
Cingulate gyrus M (PC, VOX = 80**)					
Cingulate gyrus (L)	23	6.65	−8	−14	30
Cingulate gyrus (R)	—	6.49	16	−30	31
Cingulate gyrus (L)	24	5.88	−12	−3	30
Maintenance					
Premise Processing Phase					
PFC R (NC, VOX = 74**)					
Middle frontal gyrus	8	6.34	−28	17	36
Superior frontal gyrus	9	4.60	−16	48	23
Cingulate gyrus	32	4.35	−20	25	32
Basal ganglia L (NC, VOX = 73**)					
Basal ganglia	—	5.35	24	−14	27
Basal ganglia	—	4.83	24	−34	20
Basal ganglia	—	3.74	24	−7	15

Table 4. (*continued*)

Anatomical Region	BA	t Score	Talairach Coordinates x	y	z
APFC R (NC, VOX = 51*)					
Superior frontal gyrus	10	8.32	24	44	24
Superior frontal gyrus	9	5.15	12	52	20
Middle frontal gyrus	9	3.87	28	29	28
Premise Maintenance Phase					
		No significant cluster			
Validation Phase					
Corpus callosum/basal ganglia (PC, VOX = 183***)					
Corpus callosum	—	7.29	4	16	14
Basal ganglia	—	5.74	−24	1	15
Inferior frontal gyrus	46	5.18	−32	31	6

Simple Regression Analysis: SPM(*t*)s were thresholded for height at *t* = 3.0, and cluster level $p \leq .05$, corrected for multiple comparisons. Locations, *t* scores, and Talairach coordinates refer to the peak voxels of the cluster. The correspondence of this voxel to Brodmann's areas is only established when applicable; however, note that localization can only be performed at the level of the whole cluster (the correlation of the PPC is shown in Figure 5). VOX = number of voxels; L = left; R = right; M = medial; NC = negative correlation; PC = positive correlation.

*$p \leq .05$.

**$p \leq .01$.

***$p \leq .001$.

tionship. Although a few other correlations between the BDT and the BOLD signal were found, the most important result is the negative correlation in the PPC. This correlation was also found in our previous studies, but here we show that this negative correlation of BOLD signal in the parietal cortex and visuospatial skill level only appears during the *integration phase*. Participants with higher spatial ability showed less activation in the right PPC (BA 7), as well as in left BA 7 (Table 4) only in this phase of the inference. Our results thus again support the notion that individual differences in parietal activity during model construction might reflect individual limits in neurocognitive processing resources (Reichle, Carpenter, & Just, 2000), which appear most heavily taxed during the integration phase of the inference process.

Conclusions

In sum, our study on the neurocognitive processes underlying reasoning supports the notion that reasoning can be described as a three-stage process, reflecting *premise processing*, *premise integration*, and conclusion *validation*. In this article, we identified neural
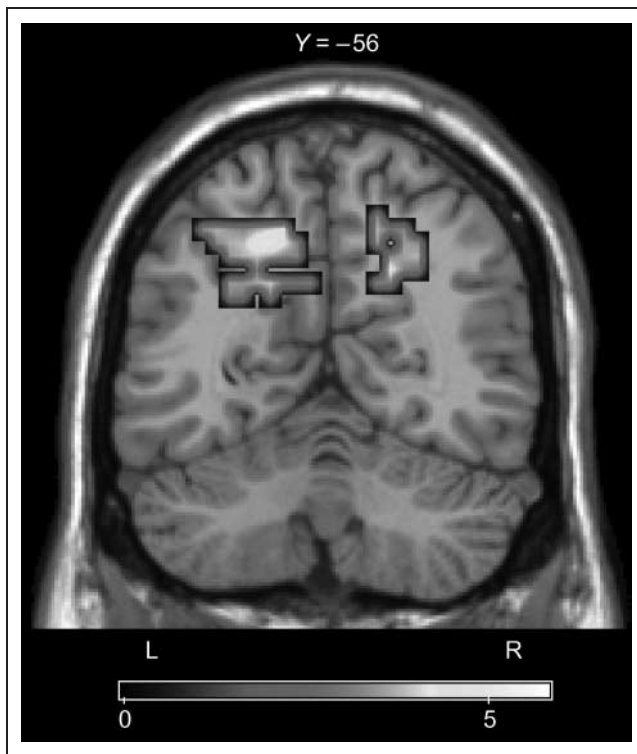
Figure 5. Negative correlation between the BOLD signal and the Block Design Test. The figure shows the negative correlation betwen individual skill differences (BDT) and the BOLD signal during the premise integration phase while the participants performed the reasoning problems. Premise integration phase: Cluster for the left and right PPC (precuneus, BA 7). The activations were significant at the cluster level calculated with SPM99 ($p \leq .05$, corrected, threshold $t = 3.0$). T score is indexed by the color bar.

structures that are specifically involved in the cognitive processes taking place in each phase. The activation in the OTC during premise processing replicates earlier results (Knauff et al., 2003; Ruff et al., 2003), which showed that problems that are easily visualized elicit activity in brain regions devoted to visuospatial processing. Premise integration and validation resulted in activation of anterior prefrontal, as well as the prefrontal and right posterior parietal cortices, respectively. We suppose that the activation in the APFC (BA 10) depends on executive demand which is necessary for the integration process (Ramnani & Owen, 2004). During the validation phase, more abstract multimodal areas in the PPC were activated for both problem types, but with activation in the right precuneus specific to reasoning. This underlines that the PPC and the PFC may be responsible and necessary for the validation of the mental models.

Our three-stage model of the neural correlates of reasoning is inspired by a strictly cognitive framework of human reasoning (Johnson-Laird, 2001). This so-called mental models theory relies on behavioral data only, but also assumes that reasoners construct visuo-spatial mental models, derive a putative conclusion

from them, and try to validate this conclusion by searching for counterexamples contradicting this conclusion (Johnson-Laird, 2001). Our present study provides neurophysiological support for three such distinct phases of reasoning, at least for deductive reasoning with spatial relations. Recently, Goodwin and Johnson-Laird (2005) have extended the theory of reasoning about relations to incorporate additional principles. One principle is called *iconicity*, which states that the structure of a model is iconic as far as possible. The OTC activation found here during the initial phase of the reasoning process is consistent with this additional principle. Because the theory of mental models claims to be a universal theory of human reasoning, these three phases may underlie all other sorts of reasoning as well, for example, syllogistic reasoning with quantifiers such as "all," "some," "none," or conditional reasoning with "if" and "than." A word of caution, however, is that the cognitive and neural processes in reasoning might depend on the nature of the problem. Reasoning with visually presented spatial relations might elicit mental models, but reasoning with other problems might evoke other processes.

METHODS

Participants

Twelve right-handed male undergraduate and graduate students (mean age 22.4, *SD* 1.98) with normal or corrected-to-normal vision (contact lenses) gave their informed consent prior to their participation in the study. None of the volunteers had any history of neurological or psychiatric disorders, or of significant drug abuse. All procedures complied with both university and hospital ethical approval.

Materials

The materials consisted of 32 reasoning and 32 maintenance problems. The reasoning problems contained two premises and a conclusion. The participants had to decide whether the conclusion necessarily followed from the premises (see Figure 1). Here is an example of a *reasoning problem* with a valid conclusion:

Premise 1:	V	X
Premise 2:	X	Z
Conclusion:	V	Z

The letter of the premises and conclusions appeared sequentially on the screen. A sentential version of the given example would be: "V is to the left of X" (first premise) and "X is to the left of Z" (second premise). From these premises, it follows "V is to the left of Z" (conclusion). Participants used an MRI-compatible re-

sponse box to indicate whether a conclusion was "True" or "False." Only the letters V, X, and Z were used, because they have almost the same black–white ratio and no problem-related words (in German) can be built from them. In the maintenance problems, the presentation of the two premises was the same as in the reasoning problem, but the participants had to decide whether the third sentence was identical to one of the previous premises or not. Thus, no inference between the two premises had to be made. Here is an example of a *maintenance problem*:

Premise 1:	V	X
Premise 2:	X	Z
Maintenance:	V	X

In this case, participants had to press the "TRUE" key, because the third sentence is an exact repetition of the first premise. Prior to each problem, an "S" or an "E" was presented for 1 sec to identify the next trial as reasoning problem ("**S**chließen" in German) or maintenance problem ("**E**rinnern" in German), respectively. The spatial relation between the two letters of each premise or conclusion was coded by placing it right or left from the midpoint of the screen. Each trial began with presentation of the first letter for 1500 msec, followed by the second letter for 1500 msec, and a pause for 1000 msec (first premise), making a total of 4 sec. The time period for the second premise and the conclusion or maintenance was the same as during the first premise. Each trial lasted for about 14 sec. In half of the premises and conclusions, the letter on the left side appeared first, followed by the letter on the right, whereas the other half were presented in the reverse order. This variation of term order is well established in reasoning research (Knauff, Rauh, Schlieder, & Strube, 1998) and prevented participants from anticipating the next letter and from drawing the conclusion during the second premise.

Behavioral Data Acquisition

Participants responded with index and middle fingers on a response box in order to record the reaction time and accuracy of each problem. Prior to the imaging study, participants were trained on 12 similar problems outside the scanner to at least 75% response accuracy.

Post-test

To examine the influence of individual differences in skill, the participants were tested after the experiment with the "BDT" from the German equivalent to the Wechsler Adult Intelligence Scale (Tewes, 1991).

Procedure and fMRI Data Acquisition

Problems were presented in an event-related design with four separate runs. Each run contained eight reasoning and eight recognition problems in a pseudo-randomized order. All problems were presented for an equal amount of time, and each premise or conclusion lasted for 4000 msec. Scanning was performed on a 1.5-T Siemens Vision scanner and the participant's head was fixed in the head coil. A mirror was placed on the coil so that participants could see a projection screen mounted on the rear of the scanner bore. All visual stimuli were projected onto this screen using a video projector. Scanner noise was reduced by headphones. Functional images were collected with a gradient-recalled echo-planar imaging (EPI) sequence, allowing the sampling of 30 parallel slices covering the whole brain [TR (repetition time): 4000 msec; TA (acquisition time): 3126 msec; TE (echo time): 60 msec; FOV (field of view): 256 mm × 256 mm in-plane resolution; $4 mm^3$ isotropic voxel size]. Eighty-five functional image volumes were collected in each of the four stimulus runs lasting 340 sec. The first two scans of each run were excluded in order for T1-effects to stabilize. A functional EPI image with 40 slices (FOV: 256 mm × 256 mm, 2 mm × 2 mm) and a sagittal T1-weighted magnetization prepared, rapid acquisition gradient-echo (MP-RAGE) image of the entire brain [160 slices, TR: 40 msec; TE: 6 msec; FA (flip angle): 40°; FOV: 256 mm × 256 mm; $1 mm^3$ isotropic voxel size] were acquired for purpose of coregistration and normalization during image preprocessing. The presentation of each stimulus (premises and conclusion) was synchronized with the TTL-pulse emitted by the scanner, and stimuli were presented with the software package "Presentation" (Presentation®, 2003).

fMRI Preprocessing

Functional and anatomical images were reoriented so that the anterior commissure corresponded to the origin of the three-dimensional standard coordinate system used in the software Statistical Parametric Mapping 99 (SPM99, 1999). The four runs for each subject were separately realigned and corrected for motion, and underwent slice timing correction. Each subject's anatomical image was coregistered with a 40-slice EPI and the functional images of each run. The parameters for spatial normalization were determined from the anatomical images of each subject, and were applied to the corresponding functional images. Images were finally smoothed with an 8-mm full-width half-maximum Gaussian kernel.

fMRI Statistical Analyses

The hemodynamic response to the premises and conclusions was modeled with event-related delta functions,

which were convolved with the canonical hemodynamic response function and its temporal derivative employed in SPM99. Low-frequency confounds were excluded from the model with a high-pass filter (192 sec cutoff), and an autoregression AR(1) model excluded the variance explained by the previous scan. The six realignment parameters for each run were included as covariates to avoid motion artifacts. If the correlation of two parameters was higher than 0.8, one of the parameters was excluded to obtain colinearity. First-level contrast images for every subject and contrast were then used for a random effects analysis to draw inferences on brain activation during the experimental problems. Only correctly answered problems were included in the analysis. All reported clusters within the conditions and the conjunction analysis are significant at the cluster level $p \leq .05$, corrected for multiple comparisons (threshold $t = 3.0$). The contrasts *within each condition* were calculated for reasoning (R): premise processing phase (Premise 2 minus Premise 1), integration phase (Premise 2 minus Conclusion), validation phase (Conclusion minus Premise 2) and maintenance (M): premise processing phase (Premise 2 minus Premise 1), maintenance phase (Premise 2 minus Premise 3), validation phase (Premise 3 minus Premise 2). Contrasts for the *conjunction analysis* were calculated with ImCalc (package within SPM99 which performs user-specific algebraic manipulations) in which the *t* value for each single contrast was compared. The following conjunction analyses were made: [(R Premise 2 minus Premise 1) and (M Premise 2 minus Premise 1)], [(R Premise 2 minus Premise 3) and (M Premise 2 minus Premise 3)], [(R Premise 3 minus Premise 2) and (M Premise 3 minus Premise 2)]. Contrasts *between the conditions* were R Premise 1 minus M Premise 1, R Premise 2 minus M Premise 2, and R Conclusion minus M Premise 3 and conversely. These contrasts were also thresholded with $t = 3.0$.

Although we calculated our model only with correctly answered problems, we used an additional analysis in order to control the difficulty discrepancy between the two problems. The second model was calculated with the reaction times as a supplementary linear parametric regressor. The contrasts were the same as before.

fMRI Region-of-Interests Analyses

The empirically derived regression parameters were extracted for each subject, problem, and phase (premises, conclusion, and maintenance) in the eight clusters that were found in the analysis between the conditions (see Figure 4). The data from each ROI were calculated in a separate 2×3 factorial ANOVA (Problem $\times$ Phase, repeated measurements). If we found significant differences in the ANOVA, we compared the relevant factor levels with paired-samples *t* tests. Significant differences between the problems within a phase are labeled with asterisks (Figure 4 bar charts and Table 3).

fMRI Correlation with the ''Block Design Test''

An additional analysis was done in SPM99 to examine the association between individual skill differences and activations while the participants performed the reasoning problems. The participants were tested after the experiment with the ''BDT'' of the German equivalent to the Wechsler Adult Intelligence Scale (HAWIE-R) (Tewes, 1991), which correlates with spatial ability. Activity for each reasoning phase was correlated with the outcome of the BDT for each participant in a simple regression RFX model.

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