Research paper Acta Neurobiol Exp 2011, 71: 479–495

# A role for the right prefrontal and bilateral parietal cortex in four-term transitive reasoning: An fMRI study with abstract linear syllogism tasks

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Previous imaging studies have identified many brain regions activated during reasoning, but there are differences among the findings concerning specific regions engaged in reasoning and the contribution of language areas. Also, little is known about the relation between task complexity and neural activation during reasoning. The present fMRI study investigated brain activity during complex four-term transitive reasoning with abstract material (determinate or partially indeterminate) and compared the resulting images to those obtained during a memorization task. The memory condition required subjects to memorize unrelated elements whereas the reasoning conditions required them to integrate information from premises and to infer relations between elements. After contrasting the two kinds of reasoning conditions with the memory condition we found that right prefrontal and bilateral parietal regions are specifically activated during reasoning. We also demonstrated that different reasoning requirements – the possibility of constructing one (determined reasoning) versus several (undetermined reasoning) models of a situation during task solving – lead to different patterns of brain activity, with higher prefrontal (PFC) activity accompanying undetermined reasoning. We interpret the PFC activity as a reflection of simultaneous maintenance and manipulation of information in reasoning. These findings provide new evidence that specific forms of reasoning (abstract and undetermined) demand recruitment of right PFC and hemispheric coordination and lend new support to the mental model theory of relational reasoning.

Key words: transitive reasoning, neuroimaging, prefrontal cortex, parietal cortex

## INTRODUCTION

Valid deductive reasoning, by definition, yields a conclusion that must be true assuming that its premises are true (Rips 1983). The deductive linear order reasoning examined in this research is based on the logic of transitivity (for reviews, see Halford, Wilson, and Phillips 1998, Leth-Steensen and Marley 2000). That is, for any A, B, and C, if A > B and B > C then it logically follows than A > C. The transitive relation denoted here by ">" might be physical (taller than), or spatial (left of), or psychological (smarter than), or formally abstract (greater than – as applied in our study). Linear order reasoning is a basic and crucial component of reasoning ability. In the simplest concrete forms this reasoning ability is possessed not only by humans since early childhood but also by monkeys, apes, and even pigeons (Delius and Siemann 1998; Halford et al. 1998) because such ability facilities adaptive predictions (which tree is the tallest? who is the most dominant?).

Linear order reasoning has long been a topic of considerable interest in cognitive and developmental psy-

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*Received 04 October 2011, accepted 08 November 2011*

Table I

Scheme of three kinds of experimental conditions – Studying Phase

| Time (s) | 0 | 5 | 10 | 14 | 19 | 23.5 | 28.5 |
|---|---|---|---|---|---|---|---|
| 1) Determinate reasoning task | Reasoning | R > T | x | T > D | x | D > S | |
| Event | Instruction | Premise 1 | isi* | Premise 2 | isi | Premise 3 | |
| 2) Indeterminate reasoning task | Reasoning | G > H | x | K > F | x | H > K | |
| Event | Instruction | Premise 1 | isi | Premise 2 | isi | Premise 3 | |
| 3) Memory task | Memory | C K | x | H J | x | B M | |
| Event | Instruction | Stimuli 1 | isi | Stimuli 2 | isi | Stimuli 3 | |

* isi (inter-stimulus interval, appearing randomly for 3.5, 4.0 or 4.5 s)

chology (e.g., Potts 1972, Rabinowitz et al. 1994, Sedek and von Hecker 2004). One of the major findings in this area refers to the generative processes of rearranging incoming piecemeal information into a comprehensive mental model (or mental array). For example, upon learning a series of pairwise pieces of information like "A > B", "B > C" and "C > D" (alphabetically ordered letters are used here to explain the idea of the paradigm, whereas random letters were used as a stimuli in real tasks), participants spontaneously rearrange these pieces of information into a coherent mental array: A > B > C > D (note that this illustrates four-term transitive reasoning, to be used in our study). Robust distance effects – where response times are found to be faster and accuracy higher for a query about A-D type relations than, for example, for a query about A-C or A-B type relations – have been pointed out as evidence of generative processes taking place during the encoding phase of such a task (Smith and Foos 1975, Leth-Steensen and Marley 2000). An "end-point effect" has been found, meaning that the distance effect is especially pronounced for the edge-most elements in the constructed array (Leth-Steensten and Marley 2000), suggesting that participants do not simply store the adjacent pairs during training. Rather, they seem to integrate all pairwise information into a unified mental model from which they can easily "read off" the answer at the moment of examination. To summarize, the distance effect in this paradigm is treated as an indicator of a spontaneous generative, constructive mental activity.

Not surprisingly, the biological network for reasoning processes has been a subject of many physiological studies. Recent imaging experiments have provided some insight into the functional neuroanatomy of deductive reasoning, but the results remain dispersed (for recent reviews, see Goel 2005, 2007). Areas mediating transitive linear reasoning were found to be distributed across the brain, including bilateral prefrontal, occipital and parietal regions as well as left lateral temporal cortex (Goel et al. 2000, Acuna et al. 2002, Goel and Dolan 2001, 2004, Kroger et al. 2002). Some authors, e.g., Knauff and colleagues (Knauff et al. 2003, Fangmeier et al. 2006), found that relational and conditional reasoning activated an occipito-parieto-frontal network, which is known to be involved in processing visuospatial information. However, other findings relate deductive reasoning with left temporal and frontal regions, which suggest that verbal code – at least in some cases – may play a mediating role during tasks requiring deduction (Acuna et al. 2002, Goel 2003, Reverberi et al. 2007).

The diversity of results regarding the neural substrates of reasoning could reflect both methodological and task variants used in experimental approaches, as well as the diversity of reasoning processes per se (Knauff et al. 2003, Goel 2005, 2007, Fangmeier et al. 2006, Goel et al. 2007). However, some progress has been made towards resolving the controversy about the neuronal processes that underlie deductive reasoning in general, with precise predictions for more specific tran-

Table II

Scheme of three kinds of experimental conditions – Testing Phase

| Time (s) | 28.5 | 33.5 | 38.5 | 43.0 | 38.0 | 42.0 | 47.0 | 50.5 | 55.5 | 59.5 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1) Determinate reasoning task | Answer | R >S ? | x | D >R ? | x | T >S ? | x | T >D ? | x | T >R ? |
| Event | Instruction | Q1<br>(end-point)<br>Yes* No | isi | Q2<br>(two-step)<br>Yes No* | isi | Q3<br>(two-step)<br>Yes* No | isi | Q4<br>(adjacent)<br>Yes* No | isi | Q5<br>(adjacent)<br>Yes No* |
| 2) Indeterminate reasoning task | Answer | G >F ? | x | K >G ? | x | H >F ? | x | K >F ? | x | H >G ? |
| Event | Instruction | Q1<br>(end-point)<br>Yes* No | isi | Q2<br>(two-step)<br>Yes No* | isi | Q3<br>(two-step)<br>Yes* No | isi | Q4<br>(adjacent)<br>Yes* No | isi | Q5<br>(adjacent)<br>Yes No* |
| 3) Memory task | Answer | H J ? | x | D T ? | x | C K ? | x | B M ? | x | R T ? |
| Event | Instruction | Q1<br>Yes* No | isi | Q2<br>Yes No* | isi | Q3<br>Yes* No | isi | Q4<br>Yes* No | isi | Q5<br>Yes No* |

* correct answer

sitivity reasoning. Namely, two specific conditions have been shown to activate the right prefrontal cortex (PFC) in a reasoning task (Fangmeier et al. 2006, Goel et al. 2009). The first right-PFC-activating condition concerns unfamiliar or nonspecific materials (lacking conceptual content, like the letters used in our study), whereas equivalent logical reasoning containing familiar materials activates only the left prefrontal cortex (Goel et al. 2000, Knauff et al. 2003). The second condition activating the right PFC (Goel et al. 2007, 2009, Prado and Noveck 2007) involves the presence of inverted relations (e.g., given that A is taller than B and B is taller than C, inferring whether C is shorter than A) or the processing of indeterminate logical relations (e.g., given A > B and A > C, assess relation B > C). In such indeterminate reasoning, not enough information is given to determine the relationship between B and C.

Our study sought to test the prediction, recently summarized by Goel (2005, 2007), that in some conditions of reasoning (i.e., more difficult, abstract, and at least partially indeterminate) right prefrontal cortex activation is sometimes necessary although not sufficient. Therefore, the main aim of this study was to examine the predicted role for the right prefrontal and bilateral parietal cortex in four-term transitive reasoning. Striving to replicate and extend existing research evidence, we applied determinate and (partially) indeterminate forms of reasoning with nonspecific material (letters). In the determinate reasoning condition, after the first two premises presentation (A> B and B> C) only one mental array might be constructed (A> B > C), and after the presentation of the third premise (C>D) this four-term mental model is slightly extended but still determined in one single way (A > B > C > D). In the indeterminate condition, on the other hand, after the presentation of the first two premises (A > B and C > D) several mental arrays might be constructed (actually four: A > B > C > D, A > C > B > D, C > D > B > A, C > A > D > B) and it is only after the presentation of the third premise (B > C) that this mental model becomes determinate as A > B > C > D and the three alternative models are rejected.

Four-term transitive reasoning (relations between four objects) is more demanding than the more simple three-term transitive reasoning used in previous studies, thus we expected recruitment not only of the right PFC but also of the bilateral parietal pathway (BA, 7) which corresponds to formal and abstract reasoning

Table III

Activation results for reasoning conditions to memory condition comparisons

| | | Talairach Coordinates | | | |
|---|---|---|---|---|---|
| Regions (Brodman area) | No. of voxels | X | Y | Z | *t*-score |
| Reasoning conditions versus memory condition – overall comparison | | | | | |
| PPC Cluster | 368*** | | | | |
| R. Precuneus (7) | | 13 | −72 | 46 | 4.79 |
| R. Precuneus (31) | | 4 | −70 | 27 | 4.45 |
| R. Precuneus (7) | | 4 | −61 | 33 | 4.38 |
| APFC Cluster | 149* | | | | |
| R. Middle frontal gyrus (10) | | 23 | 53 | 15 | 5.58 |
| Reasoning conditions *versus* memory condition – 1st premises comparison | | | | | |
| | | No significant results | | | |
| Reasoning conditions *versus* memory condition – 2nd premises comparison | | | | | |
| PPC Cluster | 121* | | | | |
| R. Precuneus (7) | | 13 | −72 | 48 | 5.32 |
| OC Cluster | 154* | | | | |
| L. Lingual gyrus (18) | | −27 | −72 | −11 | 5.03 |
| L. Inferior occipital gyrus (18) | | −34 | −85 | −10 | 4.00 |
| L. Inferior occipital gyrus (19) | | −38 | −74 | −9 | 4.49 |
| Reasoning conditions *versus* memory condition –3rd premises comparison | | | | | |
| Right PPC Cluster | 131* | | | | |
| R. Precuneus (7) | | 19 | −72 | 50 | 4.80 |
| R. Superior parietal lobule (7) | | 26 | −70 | 47 | 4.06 |
| APFC Cluster | 71*S.V.C. | | | | |
| R. Superior frontal gyrus (10) | | 23 | 54 | 13 | 4.48 |
| R. Medial frontal gyrus (10) | | 14 | 56 | 10 | 4.47 |
| R. Middle frontal gyrus (10) | | 31 | 50 | 11 | 4.05 |
| Left PPC Cluster | 157* | | | | |
| L. Precuneus (7) | | 0 | −60 | 36 | 4.34 |

$*P<0.05$; $**P<0.01$; $***P<0.001$ (corrected on cluster level, threshold, $t=3.69$); $*^{S.V.C.}$ activation significant with small volume correction only (sphere, 30 mm); (PPC) posterior parietal cortex, (APFC) anterior prefrontal cortex; (OC) occipital cortex

(Knauff et al. 2003, Goel 2005, 2007). The four-term transitive reasoning paradigm offers the possibility of evaluating whether or not the subject actually integrates information (i.e., whether she or he actively constructs a model from elements presented in the premises or just memorizes them). Note that in the three-term linear reasoning paradigm, there is only one possibility of testing simple transitive reasoning (assuming B > C and A > B, what is the relation between A and C?). Even the simplest four-term linear reasoning paradigm, on the other hand, offers three possibilities of testing integration reasoning: assuming A > B, B > C, and C > D, what are the relations (1) between A and C, (2) between B and D, and finally, (3) between A and D (the end point-relations of the mental array A > B > C > D). Therefore, questioning participants about (1) probes memory processes, whereas asking about (2) and (3) gives an opportunity to investigate integrative processes (to answer such questions correctly and fast, one needs to have in mind a fully integrated model of the relations presented).

## METHODS

### Participants

17 right-handed adult volunteers (10 women) without history of neurological disorders or chronic disease, aged 19–26 (*M* = 22.05, SD = 2.09) participated in the study. Participants were given 200 Polish zlotys (approx. €50) as compensation for their participation. All participants gave informed consent in accordance with the Ethical Review Board at the Medical University of Warsaw.

### Procedure

Task conditions

There were two experimental conditions (determinate and indeterminate reasoning) and one control condition (memory) used in this study. Each task consists of two parts: a studying phase, in which three premises (or three pairs of letters in memory condition) were presented, and a testing phase, in which five questions were asked in order to evaluate the quality of task performance. The studying phase of each task started with the presentation of an instruction indicating whether the following condition was a reasoning or memory condition. A short instruction, asking participants to answer questions, was also shown before the testing phase. The time course and examples of the reasoning and memory conditions are shown in Table I and Table II.

In the first reasoning condition, which we have called "determinate reasoning", each subsequent premise presented during the studying phase was related to the preceding one (A > B was followed by B > C, then by C > D). According to the typology proposed by Foos and colleagues (1976) this type of linear order is the easiest (90% of averaged accuracy) and requires only constructive processes of the "matching" type, which means that all presented pairs always share a common element. In the second, so called "indeterminate reasoning" condition, the participant had to keep in mind separate pieces of information which could be integrated only after receiving the information provided by the last – third – premise (A > B was followed by C > D, then by B > C). This type of linear order is much more difficult, and Foos and colleagues (1976) classified it as the "nonmatch" order type, meaning that as a model is being constructed consecutive pairs do not have any common element and they must be retained in memory separately until the third pair appears. The determinate reasoning task structure leads to one, quite obvious, model output. In the indeterminate reasoning task, on the other hand, different outputs need to be kept in mind until the third premise is presented.

In the testing phase subjects had to answer questions about the relations between the presented elements. There were three types of queries: one concerning the relationship between elements which were previously presented, so called adjacent relations (e.g., A > B?) and two about relations between elements which were not presented, so called two-step relations (e.g., A > C?) and end point relations (e.g., A > D?). Both correct (e.g., A > C, A > D) and incorrect (e.g., D > B, B > A) forms of relations between the presented letters were presented as queries. Participants had to respond whether the statement was correct or incorrect on the basis of the learned information. Note again that consecutive letters from the alphabet were used in the above explanations so as to better illustrate the idea of the paradigm, whereas random letters were used as stimuli in the actual task. The arrangement of the letters was randomized in order to minimize possible interference induced by implied alphabetical ordering of letters.

Table IV

Activation results for each reasoning condition compared to memory condition

| | | Talairach Coordinates | | | |
|---|---|---|---|---|---|
| Regions (Brodman area) | No. of voxels | X | Y | Z | *t*-score |
| Determinate reasoning condition *versus* memory condition – 1st premises comparison | | | | | |
| | | No significant results | | | |
| Determinate reasoning condition *versus* memory condition – 2nd premises comparison | | | | | |
| Right PPC Cluster | 192** | | | | |
| R. Inferior parietal lobule (7) | | 33 | −59 | 46 | 5.72 |
| R. Angular gyrus (39) | | 34 | −58 | 35 | 4.19 |
| Right PPC Cluster | 183** | | | | |
| R. Precuneus (7) | | 13 | −72 | 48 | 5.56 |
| R. Precuneus (7) | | 2 | −61 | 35 | 4.39 |
| Determinate reasoning condition *versus* memory condition – 3rd premises comparison | | | | | |
| Right PPC Cluster | 134** | | | | |
| R. Precuneus (7) | | 2 | −63 | 36 | 5.22 |
| Indeterminate reasoning condition *versus* memory condition – 1st premises comparison | | | | | |
| | | No significant results | | | |
| Indeterminate reasoning condition *versus* memory condition – 2nd premises comparison | | | | | |
| | | No significant results | | | |
| Indeterminate reasoning condition *versus* memory condition – 3rd premises comparison | | | | | |
| Left OC Cluster | 228*** | | | | |
| L. Middle occipital gyrus (19) | | −31 | −81 | 9 | 5.95 |
| L. Middle occipital gyrus (19) | | −38 | −72 | 11 | 4.75 |
| Right APFC Cluster | 204*** | | | | |
| R. Superior frontal gyrus (10) | | 16 | 60 | 23 | 5.19 |
| R. Superior frontal gyrus (10) | | 20 | 58 | 10 | 5.01 |
| R. Middle frontal gyrus (10) | | 23 | 53 | 15 | 5.01 |

*$P<0.05$; **$P<0.01$; ***$P<0.001$ (corrected on cluster level, threshold, $t$=3.69); (PPC) posterior parietal cortex, (APFC) anterior prefrontal cortex; (OC) occipital cortex

The memory condition required subjects to memorize three pairs of unrelated elements, e.g., after the presentation of the three pairs of objects G T; U R; W S; the subject was asked whether a presented pair of letters had been shown before or not (e.g., G T ? – with the proper answer "yes", or F H ? – with proper answer "no"). The structure of the reasoning and memory conditions was very similar, but in the memory task there was no possibility, at any moment, of integrating the presented information.

Every premise or query was presented for 5 seconds, with the fixation point (inter-stimulus interval) between them appearing pseudorandomly (in a fixed order for each participant) for 3.5; 4 or 4.5 seconds (see Table I). Brain activity was analyzed during the learning phase of each task, in which subjects were required to create a mental representation of the stimuli by integrating the incoming information (in the reasoning conditions) or just to maintain the information (in the memory condition).

Participants responded (choosing a yes or no option) with the thumb of their right (dominant) hand on a response pad. We recorded the reaction time and accuracy of each response. Prior to the imaging study, participants were trained on similar tasks outside the scanner (achieving approx. 80% overall accuracy).

### Stimuli

In all tasks we used capital letters as stimuli instead of whole sentences in order to avoid linguistic connotations. In tasks requiring reasoning, a symbol indicating the relation between the elements (">") was additionally presented. All stimuli were back projected onto a transparent screen placed in the magnet room. Stimuli were presented with the ''Presentation'' software package (Presentation 11.0, www.neurobs.com) and the presentation of each stimulus (premises and conclusions) was synchronized with the pulse emitted by the scanner.

### fMRI procedure

Participants performed 15 tasks (5 "determinate", 5 "indeterminate", and 5 control memory tasks). Each task consisted of three premises presented in a studying phase and five queries asked during a testing phase (details about studying phase

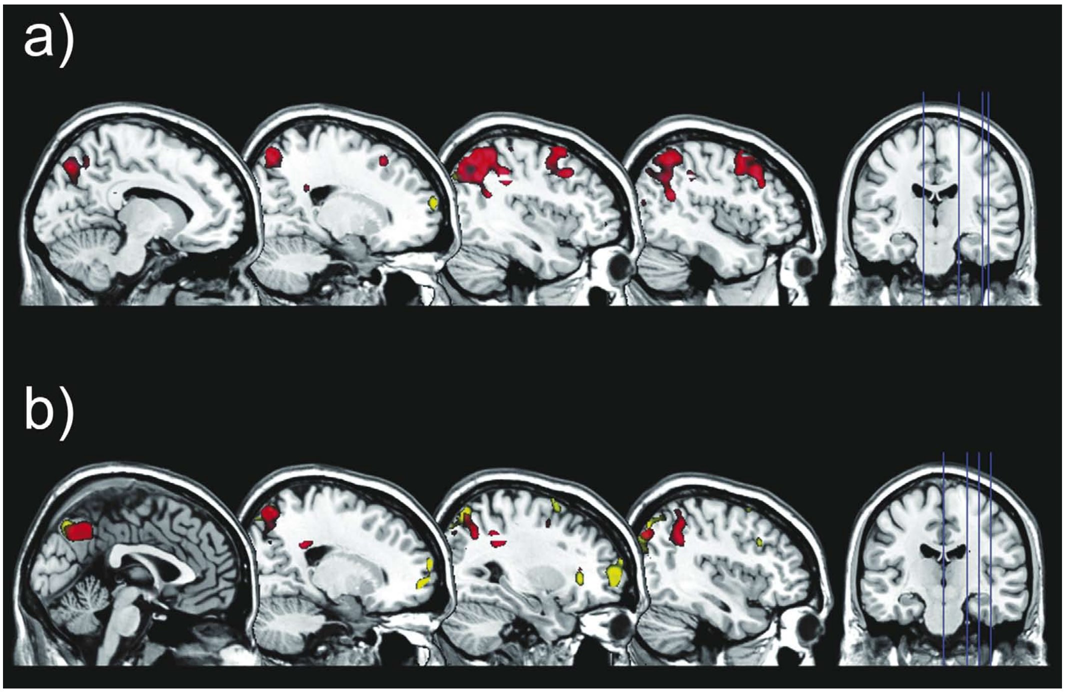

Fig 1. Activation results for determinate reasoning (red color) and indeterminate reasoning (yellow color) conditions during second (a) and third (b) premise processing. For each reasoning task, a memory task served as a control condition ($P<0.05$, cluster-level corrected).

Table V

Activation results during determinate reasoning condition (A > B – B > C – C > D)

| | | Talairach Coordinates | | | |
|---|---|---|---|---|---|
| Region (Brodman area) | No. of voxels | X | Y | Z | *t*-score |
| Premise 2 – Premise 1 | | | | | |
| | | No significant results | | | |
| Premise 3 – Premise 1 | | | | | |
| PPC Cluster | 166 * | | | | |
| R. Parietal lobe (39) | | 30 | −58 | 39 | 5.53 |
| R. Superior parietal lobule (7) | | 24 | −64 | 40 | 5.30 |

*$P<0.05$; **$P<0.01$; ***$P<0.001$ (corrected on cluster level, threshold, $t$=3.69); (PPC) posterior parietal cortex

are shown in Table I and these concerning studying phase in Table II). A total of 45 trials from studying phase were entered into an event-related design matrix. The analysis of brain activity was performed on the signal registered during the studying phase only, as we were especially interested in processes underlining mental model construction, not validation.

### Processing of fMRI data

#### Imaging data acquisition

Imaging was performed using an 8-channel phased-array coil on a 1.5-Tesla GE scanner (GE Healthcare, Poland) at the Department of Nuclear Medicine of Bródno Hospital in Warsaw (Poland). After acquisition of a T2 localizer scan, functional run was collected (TR = 3000 ms, TE = 50 ms, 28 axial slices, slice thickness = 4 mm, spacing = 0.5 mm, matrix = 96 × 96, field of view = 240 mm, the whole experiment lasted 18 minutes and 32 seconds during which 370 volumes were collected).

#### fMRI data preprocessing and analysis

SPM5 (http://www.fil.ion.ucl.ac.uk/spm/) was used to perform all pre-processing and data analysis steps. Standard pre-processing was performed on the functional data, including motion correction (with unwrapping option), normalization with SPM5 EPI template and spatial smoothing using an 8 mm full-width half maximum (FWHM) Gaussian kernel. Statistical analyses were performed on the individual and group level using the General Linear Models (Friston et al. 1995). The hemodynamic response related to the presented premises of each task was modeled with event-related delta functions, which were convolved with the canonical hemodynamic response function and its temporal and dispersion derivatives employed in SPM5. First-level contrast images for every subject and second-level contrasts for the whole group of participants were then used for a random effects analysis to draw inferences on brain activation during the experimental tasks. All reported clusters within the conditions and the conjunction analysis are significant at the cluster level $P<0.05$, corrected for multiple comparisons (cluster size > 15 voxels). Only main peaks of activation with Z-score within each cluster are reported and the brain structures they correspond to. Numbers of voxels activated in significant clusters are presented in subsequent tables with results. The MINI coordinates were translated to Talairach space using the icbm2tal algorithm (Lancaster et al. 2007) with the GingerALE 1.1 application (www.brainmap.org). Then TalairachClient 2.4.2 was used to name the activated structures (Lancaster et al. 2000; www.talairach.org).

Table VI

Activation results during indeterminate reasoning condition (A>B – C>D – B>C)

| | | Talairach Coordinates | | | |
|---|---|---|---|---|---|
| Region (Brodman area) | No. of voxels | X | Y | Z | $t$-score |
| Premise 2 – Premise 1 | | | | | |
| No significant results | | | | | |
| Premise 3 – Premise 1 | | | | | |
| Right PFC Cluster | 2499 *** | | | | |
| R. Superior frontal gyrus (6) | | 28 | −6 | 65 | 9.32 |
| R. Middle frontal gyrus (8) | | 50 | 14 | 37 | 8.9 |
| R. Middle frontal gyrus (6) | | 32 | −6 | 46 | 8.39 |
| Right subcortical Cluster | 477*** | | | | |
| R. Lentiform nucleus (-) | | 23 | 19 | −1 | 8.27 |
| R. Claustrum (-) | | 29 | 16 | 13 | 6.58 |
| Bilateral PFC Cluster | 2786*** | | | | |
| R. Superior frontal gyrus (6) | | 4 | 9 | 48 | 7.89 |
| L. Precentralgyrus (6) | | −52 | −4 | 46 | 7.40 |
| L. Superior frontal gyrus (6) | | −2 | 8 | 53 | 7.25 |
| Left PPC Cluster | 1036*** | | | | |
| L. Inferior parietal lobule (40) | | −42 | −47 | 41 | 6.92 |
| L. Supramarginalgyrus (40) | | −40 | −42 | 34 | 6.19 |
| L. Superior parietal lobule (7) | | −30 | −60 | 47 | 5.55 |
| Right PPC Cluster | 926*** | | | | |
| R. Superior parietal lobule (7) | | 32 | −56 | 41 | 6.34 |
| R. Precuneus (7) | | 22 | −63 | 36 | 5.59 |
| R. Inferior parietal lobule (40) | | 39 | −53 | 45 | 4.83 |

*$P<0.05$; **$P<0.01$; ***$P<0.001$ (corrected on cluster level, threshold, $t=3.69$); (PPC) posterior parietal cortex, (PFC) prefrontal cortex

## RESULTS

### Behavioral data

A repeated measure ANOVA using a 2 × 3 design (2 types of reasoning task: determinate *versus* indeterminate; and three query types: adjacent *versus* two-step versus end-point) conducted on accuracy data showed only one significant main effect of query type, $F_{2,32}=7.87$; $P<0.01$; $\eta^2=0.330$. Main effect of reasoning task and query type by task type interaction effect were not significant, $F_{1,16}=3.43$; $P<0.1$; $\eta^2=0.176$ and $F_{2,32}=2.99$; $P<0.1$; $\eta^2=0.157$, respectively. *Post-hoc* analysis (with Bonferroni correction, $P<0.05$) revealed differences between accuracy for two-step (0.77) and end-point (0.89) as well as between two-step and adjacent (0.88) relations, which supports the involvement of active

Table VII

Activation results during maintenance condition

| Region (Brodman area) | No. of voxels | Talairach Coordinates X | Talairach Coordinates Y | Talairach Coordinates Z | *t*-score |
|---|---|---|---|---|---|
| Premise 2 – Premise 1 | | | | | |
| No significant results | | | | | |
| Premise 3 – Premise 1 | | | | | |
| Left FC Cluster | $120^{\#}$ | | | | |
| L. Medial frontal lobe (6) | | −7 | −5 | 61 | 5.01 |

*$P<0.05$; **$P<0.01$; ***$P<0.001$ (corrected on cluster level, threshold, $t=3.69$); (FC) frontal cortex

generative processes during the solution of a linear syllogism of this type.

In order to establish how performance of reasoning tasks differ from memory task (which mean accuracy was 0.94) in next step we performed one-way repeated measures ANOVA with memory task vs. adjacent vs. two-steps vs. end point relations as factor levels. This analysis was statistically significant, $F_{3,48}=8.96$; $P<0.01$ (with Greenhouse-Geisser correction) and *post-hoc* test (with Bonferroni correction, $P<0.05$) showed that level of accuracy for two-step relations was significantly lower than the accuracy levels of the three other relations (memory, adjacent and end-point).

Additional ANOVA conducted on response times revealed a significant main effect of query type, $F_{2,32}=3.75$; $P<0.05$, $\eta^2=0.190$ as well as of query type by task type interaction effect, $F_{2,32}=5.64$, $P<0.01$, $\eta^2=0.260$. The main effect of task type was not statistically significant, $F_{1,16}=1.48$, ns. $\eta^2=0.085$. The simple effects analysis showed that determinate and indeterminate reasoning tasks differed only in terms of reaction times for the queries about end-point relations.

## Functional imaging data

In the first step we focused our analyses on comparing brain activity between the two reasoning conditions and the control memory condition. This is a well-known strategy for obtaining information about the brain structures activated by processes of interest (Wager and Smith 2003) and this kind of analysis enabled us to compare the results with other, similarly done studies. In subsequent steps more detailed comparisons were performed, which focused on differentiating the structures engaged specifically in determinate or indeterminate reasoning.

### Between tasks comparisons

Reasoning *versus* memory. To assess the general pattern of brain activity that accompanies the solving of linear syllogism tasks, we compared brain activity during the two reasoning conditions to the control condition (all premises from the two reasoning tasks were modeled as one type of stimuli and compared to all memory trials within one contrast). As shown in Table III, this comparison revealed two brain regions with higher activation: the right anterior prefrontal cortex (APFC) and right posterior parietal cortex (PPC).

The more detailed analysis, contrasting each premise from reasoning trials to corresponding memory trials, revealed certain dynamics in terms of hemodynamic response. We did not observe any differences between reasoning and memory trials during processing of the first premises, parietal regions were seen to be significantly more active during second and third

Table VIII

| Comparisons with exclusive masking procedure | | | | | |
|---|---|---|---|---|---|
| | | Talairach Coordinates | | | |
| Region (Brodman area) | No. of voxels | X | Y | Z | *t*-score |
| Indeterminate reasoning *versus* memory condition contrasts masked by determinate reasoning *versus* memory | | | | | |
| Premise 1 | | | | | |
| | | No significant results | | | |
| Premise 2 | | | | | |
| | | No significant results | | | |
| Premise 3 | | | | | |
| APFC Cluster | 92*$^{FDR}$ | | | | |
| R. Middle frontal gyrus (10) | | 25 | 51 | 17 | 4.46 |
| Determinate reasoning *versus* memory condition contrasts masked by indeterminate reasoning *versus* memory | | | | | |
| Premise 1 | | | | | |
| | | No significant results | | | |
| Premise 2 | | | | | |
| PPC Cluster | 367** | | | | |
| R. Angular gyrus (39) | | 32 | −63 | 31 | 3.77 |
| R. Superior parietal lobule (7) | | 34 | −61 | 46 | 3.68 |
| R. Precuneus (19) | | 33 | −71 | 38 | 3.62 |
| Premise 3 | | | | | |
| | | No significant results | | | |

*$P<0.05$; **$P<0.01$; ***$P<0.001$ (corrected on cluster level, threshold, $t=3.69$); (FDR) contrast significant with FDR correction for multi-comparisons; (PPC) posterior parietal cortex; (APFC) anterior prefrontal cortex

premise processing, whereas frontal regions showed higher activity in reasoning trials only during processing of third premises. All significant differences are listed in detail in Table III.

Determinate and indeterminate reasoning *versus* memory. Further analysis was conducted to assess brain activity during each of the reasoning conditions used in the study. Comparison of determinate reasoning to the control condition revealed activation of a large portion of the posterior parietal areas (PPC). The detailed comparisons of each premise showed that this enhanced parietal activity is visible during second and third premise presentation. The same analysis conducted for indeterminate reasoning trials revealed a different pattern of brain activity. We observed differences between this type of reasoning and memory conditions mainly within anterior prefrontal regions. Even more importantly, we obtained this dissimilarity during third premise presentation only – see Figure 1 and Table IV for details.

The direct comparison of determinate and indeterminate conditions revealed only one significant difference during second premise presentation. There were higher brain activity within the right cingulated gyrus and part of the limbic lobe (BA31; comparison significant on cluster level, no. of voxels = 143) in the determinate reasoning condition.

## Within-task comparisons

In order to establish the course of brain activity during each type of reasoning and memory conditions we performed a series of within-task comparisons, in which we performed the following contrasts: Premise 2 *versus* Premise 1 and Premise 3 *versus* Premise 1.

Determinate reasoning task. There was no statistically significant difference in comparison of Premise 2 *versus* Premise 1. A small cluster of enhanced activity within the parietal lobe was obtained for the Premise 3 *versus* Premise 1 comparison. Details are presented in Table V.

Indeterminate reasoning task. Results for the indeterminate reasoning condition are listed in Table VI. We did not observe any significant differences in brain activity between second and first premise presentation. Pronounced and highly significant differences appeared when we compared Premise 3 with Premise 1– higher brain activation was observed in bilateral occipital, parietal, and frontal regions during third premise presentation.

Maintenance task. We conducted the same set of contrasts for the maintenance condition, which revealed partial overlap with the results for the indeterminate reasoning condition. For the Premise 2 to Premise 1 comparison there were no differences, but for the Premise 3 *versus* Premise 1 contrast we obtained significantly higher activity for Premise 3 in the middle frontal region (BA6). Detailed results are listed in Table VII.

## Masked contrasts

In order to determine which areas are specifically involved in each kind of reasoning, we performed comparisons by the exclusive masking procedure. To identify the areas exclusively activated by indeterminate reasoning we masked the contrast of determinate reasoning *versus* memory by the contrast of indeterminate reasoning versus memory. This exclusive masking procedure was performed for each premise separately and showed only a single – but highly significant – result, namely higher anterior prefrontal cortex involvement during third premise presentation in indeterminate reasoning tasks (see Table VIII).

The same procedure for determinate reasoning task (masked exclusively by indeterminate reasoning task) revealed significant activities only during second premise presentation, with higher posterior parietal engagement in determinate reasoning (see Table VII).

## Conjunction analyses

We also performed a series of conjunction analyses – for all comparisons, contrasting each reasoning premise to its memory analogue. We did not observe any significant effects for conjunction analysis of first, second, or third premise contrasts but we hypothesized that there should be some overlap in brain areas mediating the integration process. To test this hypothesis, a small volume correction (SVC) (Worsley et al. 1996, Friston 1997) approach was applied to compare two "integrative" points of our reasoning tasks (namely, the second premise in the determinate reasoning condition and the third premise in the indeterminate reasoning condition) in conjunction analysis. This analysis reveled a PPC cluster with 182 voxels, significant at $P<0.05$. The result of this analysis is consistent with previously obtained results from exclusive masking procedure and is also visible in pattern of activity presented in Figure 1.

## DISCUSSION

This study has shown that specific regions of the prefrontal (right APFC) and parietal (bilateral PPC) cortex are engaged in a relatively complex and abstract transitive reasoning task and provides new evidence that specific forms of reasoning differ depending on the possibility of integration of information. Indeterminate reasoning condition, with delayed time of possible information integration, demanded recruitment of both right PFC and bilateral PPC, whereas determinate reasoning condition (in which integration of information takes place immediately after each premise presentation) – an apparently similar mental activity, albeit without such an explicit maintenance and manipulation component – recruited mainly parietal structures.

It has yielded compelling evidence, extending and supporting a-priori predictions based on the research of Vinod Goel, Markus Kanuff and their associates (Knauff et al. 2003, Goel 2005, 2007, Goel et al 2007, 2009), that specifically the right anterior prefrontal (APFC), right dorsolateral prefrontal cortex (DLPFC), and bilateral posterior parietal cortex (PPC) play a crucial role in four-term transitive reasoning. These findings, especially stressing an involvement of the prefrontal cortex, have a solid basis in the existing literature concerning neural correlates of relational reasoning (see Introduction). They are also congruent with observations of patients with damage to prefrontal areas that show impaired performance of any sort of reasoning tasks requiring the integration of relations, but perform memory tasks normally (Waltz et al. 1999, Goel et al 2007). Additionally, we have provided new evidence that specific forms of reasoning (abstract, complex, and indeterminate) demand recruitment of right PFC and hemispheric coordination and lent new support to the mental model theory of relational reasoning.

### Prefrontal cortex and reasoning processes

The prefrontal cortex is the most often reported area involved in different types of reasoning processes (e.g., Gilbert et al. 2006, Christoff et al. 2009) and dedicated to fulfilling distinct mental processes (Fuster 2008). The role of the PFC in reasoning has been highlighted also in several studies of relational complexity and integration; specifically, anterior PFC activation was associated with relational integration and also with the integration of information into a mental model (Acuna et al. 2002).

Activation of the lateral part of APFC (BA 10), also known as the rostrolateral prefrontal cortex (RLPFC), is often reported in studies concerning the use of abstract rules (e.g., during different types of reasoning or problem solving, Christoff and Gabrieli 2000), during simultaneous integration of multiple relations, in multiple-task coordination, working memory tasks (Waltz et al. 1999, Goel 2005, 2007, Gilbert et al. 2006) as well as during maintenance of information from multiple domains and integration of cross-domain information (Postle and D'Esposito 1999, Smith and Jonides 1999, Fuster et al. 2000). The meta-analysis conducted by Wager and Smith (2003) showed that tasks requiring greater involvement of manipulation – treated as an executive function, primarily involved in operations on stimuli while maintaining items in working memory – produced increases of activity in APFC mainly in the right hemisphere (Wager and Smith 2003). The DLPFC, on the other hand, was shown to be mostly active during tasks with continuous updating of information or with memory about temporal order of information, but not during tasks requiring manipulation of information (Wager and Smith 2003).

The complex reasoning task used in our study, which elicited activity in APFC, not only required a participant to bind pieces of information into a coherent structure (which is also present in the simple reasoning condition) but was also highly demanding in terms of dealing with many processes simultaneously – building a mental model about the presented relations required the subject not only to keep pieces of information in their working memory, but also to manipulate and integrate the presented elements. This multi-tasking component probably finds reflection in the observed high APFC activity.

Our results are also in agreement with the common distinction between ventral and dorsal streams of information processing for object and spatial material, respectively. What is especially interesting in the light of our results is that within the frontal cortex, spatial working memory tasks activate the superior DLPFC or the superior frontal areas (Courtney et al. 1998), whereas object working memory tasks increase neural activity more in the mid- and inferior frontal regions (Wager and Smith 2003). Our reasoning tasks, being spatial in nature, should therefore elicit activity within the dorsal or superior frontal regions – which was found to be true, although only in the case of more demanding, indeterminate reasoning condition.

## Parietal cortex and reasoning processes

The neural enhancement within parietal areas obtained in our study was especially visible in the precuneus, a region of associative cortex which shares connections with many cortical and subcortical areas (Cavanna and Trimble 2006). Importantly, the precuneus also has reciprocal cortical connections with the prefrontal cortex (Cavanna and Trimble 2006). Given that the PFC and PPC are reciprocally connected it is not surprising that these areas may cooperate during solving demanding tasks like linear syllogisms, requiring manipulation and integration of spatially organized material.

We identified three regions within the precuneus (BA7, BA19 and BA31) which could play a distinct role in the process of information integration during spatial reasoning. The regions active in both reasoning conditions – BA 7 and BA 31 (when the two reasoning tasks are compared to the memory condition) were reported as being involved in spatial working memory and imagery. In addition, BA7 activates during the location of objects in space, orientation, and sustained attention (Cabeza and Nyberg 2000) as well as during updating and manipulating of working memory content (Wager and Smith 2003). The third region of the precuneus that showed enhanced activity during determinate, but not the indeterminate, reasoning task was BA 19. The activity within this region was attributed in previous studies to spatial memory and imagery as well as to spatial and object working memory and integration of multimodal information (Cabeza and Nyberg 2000).

In our study, parietal enhancement was observed during both reasoning tasks (although it was more pronounced in the simple reasoning condition), leading to the conclusion that a mental process present in both types of syllogism we used caused this activity. Results of conjunction analyses demonstrated similarities between the two tasks during second (in determinate) and third (in indeterminate) premise presentation. It seems reasonable to hypothesize that a particular mechanism with its neural underpinning in the parietal activity takes place earlier in the determinate than in the indeterminate reasoning condition. One candidate for this process is the integration of incoming, piecemeal information, which is possible earlier in determinate than in indeterminate reasoning tasks.

What differentiated the two reasoning conditions was the activity within frontal areas accompanying PPC activity. The additional APFC activity in the complex (partially undetermined) reasoning condition could be a result of the need to simultaneous manipulate and integrate material kept in working memory. So, the involvement of APFC seems to be especially important when a conclusion needs to be drawn from premises, which require manipulation of information. When the task does not require rearrangement of the order of information (but still requires integration and updating of information, like in the simple reasoning condition) we do not observe involvement of APFC areas. This leads to the conclusion that APFC activity during the solution of linear syllogisms is related to the process of information manipulation. It seems that for integrating spatial information and for reasoning processes based on mental models, in particular when reasoning problems involve a one-model solution (a simple reasoning condition), the activity of the parietal cortex plays the most important role, a finding that is in line with results of many other studies (for review see: Goel 2005, 2007, Knauff 2009). In addition, when reasoning complexity increases, it leads to greater activation in the anterior part of the PFC as well as in the parietal cortex (Kroger et al. 2002).

Several animal studies confirm such an interpretation of simultaneous prefrontal and parietal activations, and also stress the role of parietal regions in reasoning and decision making. In a review of the neural underpinnings of the executive functions in monkeys, Stoet and Snyder (2009) emphasize that activity of neurons in the PPC may reflect abstract rule processing and be involved in the decision-making process.

## The nature of reasoning

Moreover, our results additionally bear upon one longstanding debate concerning the nature of reasoning processes (Sternberg 1980, Knauff et al. 2003, Goel 2005). The two opposing theories in this debate – the mental model theory and mental logic theory – make strict predictions about the neural substrate underlying syllogistic reasoning. The mental model theory (Johnson-Laird et al. 1992, Johnson-Laird 1983) proposes that transitive reasoning crucially involves processes such as constructing and manipulating spatially organized mental models. The predictions made by the mental model theory assume that neural structures for visuo-spatial processing, such as parieto-occipital areas of the right hemisphere, should contribute most to deductive – and especially relational – reasoning. The mental logic theory, on the other hand, maintains that transitive reasoning crucially involves sets of abstractive rules which are used to "translate" premises into the inner language of mental logic. As verbal code is seen as required during this translation, this theory is also called the linguistic hypothesis (Clark 1969, Braine and O'Brien 1998). It predicts that regions connected to language processing – especially the left temporal lobe and left inferior frontal lobe – should be activated during the solution of reasoning tasks. The results of our study are clearly in favor of a mental model theory of relational reasoning (Johnson-Laird 2001) as it predicts that reasoning trials should result in enhanced right hemisphere activation, especially in parietal areas.

When discussing the neural underpinnings of reasoning processes it is very important to take into account the material used as stimuli. Some authors have shown that reasoning with abstract premises or belief-neutral material involves the right hemisphere, whereas reasoning with concrete, belief-laden or familiar material relies on processing in the left hemisphere (Knauff et al. 2003, Goel 2005, 2007, Fangmeier et al. 2006, Goel et al. 2007, 2009). As we used relatively complex (four-term), abstract material, our findings falsify the linguistic model of reasoning in its extreme form, according to which language processes should accompany any kind of reasoning.

What distinguishes our study from previous experiments on the neuroimaging of reasoning is the possibility of distinguishing between immediate and delayed information integration, which we achieved by employing a specially designed four-term – instead of the more popular three-term – linear order task. To our knowledge, the study presented in this article is the first to consider such a differentiation in reasoning processes in the neuroimaging context. In some previous studies authors used syllogisms with even more than four terms (e.g. Hinton et al. 2010) but without manipulating the order of premise presentation (they always had the determinate type of reasoning), which made it impossible to distinguish between conditions more and less favourable for spontaneous integration. However, the rearrangement of the order of premises ($A > B$, $C > D$, $B > C$) importantly changes the reasoning process. The first two premises cannot be integrated (needing to be kept in working memory) and the integrating process is "delayed" until the presentation of the third premise that enables the four-term mental array to be generated in full form. This important differentiation between immediate (in determinate) and delayed (in indeterminate) reasoning was earlier recognized as important factor in behavioral research, for example in studies of reasoning limitations in aging and depression (Sedek and von Hecker 2004). To our knowledge, such a distinction has not yet been clearly assimilated in the search for the neural systems involved in reasoning processes.

## CONCLUSIONS

In this study we found that different reasoning requirements – the possibility of constructing one (determined reasoning) versus several (undetermined reasoning) models of a situation during task solving – lead to different patterns of brain activity. During both type of reasoning parietal activity was observed but only undetermined reasoning conditio was accompanied by higher prefrontal (PFC) activity. Our results offer better insight and allow for the integration of previous behavioral and neuroimaging findings on higher-order mental processes (Goel et al. 2009, Halford et al. 2010, Revet-ben et al. 2010, Prado et al. 2011). In the interdisciplinary area of thinking and reasoning there is now broader acceptance of the idea that some of the involved processes are relatively spontaneous (like on-line transitive reasoning, text comprehension and in our study determined reasoning) and some more deliberative (like delayed transitive reasoning, classical syllogisms, or reasoning about indeterminate relations). We interpret the enhanced PFC activity during indeterminate reasoning condition as a reflection of simultaneous maintenance and manipulation of information in reasoning proces.

## ACKNOWLEDGEMENTS

Support for the research reported herein came from grant from the Polish Ministry of Science and Higher Education (N106 017 31/1344).

We are grateful to Prof. Małgorzata Kossut for providing thoughtful remarks and suggestions regarding earlier versions of the manuscript. A.B. is indebted to Prof. Richard Frackowiak for hosting her at the Functional Imaging Laboratory, Welcome Trust Centre for Neuroimaging, University College London during the may 2008, and to dr Bogdan Draganski for helping with functional neuroimaging data analysis.

## REFERENCES

Acuna BD, Eliassen JC, Donoghue JP, Sanes JN (2002) Frontal and parietal lobe activation during transitive inference in humans. Cereb Cortex 12: 1312–1321.

Braine MDS, O'Brien DP (Eds) (1998) Mental Logic. Lawrence Erlbaum Associates, Mahwah, NJ.

Cabeza R, Nyberg L (2000) Imaging cognition II: An empirical review of 275 PET and fMRI studies. J Cogn Neurosci 12: 1–47.

Cavanna AE, Trimble MR (2006) The precuneus: a review of its functional anatomy and behavioural correlates. Brain 129: 564–583.

Clark HH (1969) Linguistic processes in deductive reasoning. Psychol Rev 76: 387–404.

Christoff K, Gabrieli J (2000) The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within human prefrontal cortex. Psychobiology 28: 168–186.

Christoff K, Keramatian K, Alan GM, Smith R, Maedler B (2009) Representational topography in lateral prefrontal cortex according to levels of abstraction. Brain Res 1286: 94–105.

Courtney SM, Petit L, Maisog JM, Ungerleider LG, Haxby JV (1998) An area specialized for spatial working memory in human frontal cortex. Science 279: 1347–1351.

Delius JD, and Siemann M (1998) Transitive responding in animals and humans: exaption rather than adaption. Behav Process 42: 107–137.

Fangmeier T, Knauff M, Ruff CC, Sloutsky V (2006) fMRI evidence for a three-stage model of deductive reasoning. J Cogn Neurosci 18: 320–334.

Foos PW, Smith KH, Sabol MA, Mynatt BT (1976) Constructive processes

in simple linear order problems. J Exp Psychol Hum Learn 2: 759–766.

Friston KJ, Holmes AP, Worsley KJ, Poline JB, Frith C, Frackowiak RSJ (1995) Statistical Parametric Maps in Functional Imaging: A General Linear Approach. Hum Brain Mapp 2: 189–210.

Friston KJ (1997) Testing for anatomical specified regional effects. Hum Brain Mapp 5: 133–136.

Fuster JM, Bodner M, Kroger JK (2000) Cross-modal and cross-temporal association in neurons of frontal cortex. Nature 405: 347–351.

Fuster JM (2008) The Prefrontal Cortex (4rd ed.). Academic Press, Boston, MT.

Gilbert SJ, Spengler S, Simons JS, Steele JD, Lawrie SM, Frith CD, Burgess PW (2006) Functional specialization within rostral prefrontal cortex (area 10): A meta-analysis. J Cogn Neurosci 18: 932–948.

Goel V, Buchel C, Frith C, Dolan R (2000) Dissociation of Mechanisms Underlying Syllogistic Reasoning. NeuroImage 12: 504–514.

Goel V, Dolan RJ (2001) Functional neuroanatomy of three-term relational reasoning Neuropsychologia. 39: 901–909.

Goel V (2003) Evidence for dual neural pathways for syllogistic reasoning. Psychologica 32: 301–309.

Goel V, Dolan RJ (2004) Differential involvement of left prefrontal cortex in inductive and deductive reasoning. Cognition 93: 109–121.

Goel V (2005) Cognitive neuroscience of deductive reasoning. In: Cambridge Handbook of Thinking and Reasoning (Holyoak K, Morrison R, Eds). Cambridge University Press, Cambridge, MT. p. 475–492.

Goel V (2007) Anatomy of deductive reasoning. Trends Cogn Sci 11: 435–441.

Goel V, Tierney M, Sheesley L, Bartolo A, Vartanian O, Grafman J (2007) Hemispheric specialization in human prefrontal cortex for resolving certain and uncertain inferences. Cereb Cortex 17: 2245–2250.

Goel V, Stollstorff M, Nakic M, Knutson K, Grafman G (2009) A role for right ventrolateral prefrontal cortex in reasoning about indeterminate relations. Neuropsychologia 47: 2790–2797.

Halford G, Wilson W, Phillips S (1998) Processing capacity defined by relational complexity: Implications for comparative, developmental, and cognitive psychology. Behav Brain Sci 21: 803–863.

Halford GS, Wilson WH, Phillips S (2010) Relational knowledge: The foundation of higher cognition. Trends Cogn Sci 14: 497–505.

Hinton EC, Dymond S, Von Hecker U, Evans CJ (2010) Neural correlates of relational reasoning and the symbolic distance effect: Involvement of parietal cortex. Neuroscience 168: 138–148.

Johnson-Laird PN (1983) Mental models: Towards a Cognitive Science of Language Inference and Consciousness. Cambridge University Press, Cambridge, UK.

Johnson-Laird PN, Byrne RMJ, Schaeken W (1992) Propositional reasoning by model. Psychol Rev 99: 418–439.

Johnson-Laird PN (2001) Mental models and deduction. Trends Cogn Sci 5: 434–442.

Knauff M, Fangmeier T, Ruff CC, Johnson-Laird PN (2003) Reasoning models and images: Behavioral measures and cortical activity. J Cogn Neurosci 15: 559–573.

Knauff M (2009) A Neuro-cognitive theory of deductive relational reasoning with mental models and visual images. Spat Cogn Comput 9: 109–137.

Kroger JK, Sabb FW, Fales CL, Bookheimer SY, Cohen MS, Holyoak KJ (2002) Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: a parametric study of relational complexity. Cereb Cortex 12: 477–485.

Lancaster JL, Woldorff MG, Parsons LM, Liotti M, Freitas CS, Rainey L, Kochunov PV, Nickerson D, Mikiten SA, Fox PT (2000) Automated Talairach Atlas labels for functional brain mapping. Hum Brain Mapp 10: 120–131.

Lancaster JL, Tordesillas-Gutierrez D, Martinez M, Salinas F, Evans A, Zilles, K, Mazziotta JC, Fox PT (2007) Bias between MNI and Talairach coordinates analyzed using the ICBM-152 template. Hum Brain Mapp 28: 1194–1205.

Leth-Steensen C, Marley AJ (2000) A model of response time effect in symbolic comparison Psychol Rev 107: 62–100.

Postle BR, D'Esposito M (1999) What–then–where in visual working memory: an event-related fMRI study. J Cogn Neurosci 11: 585–597.

Potts GR (1972) Information processing strategies used in the encoding of linear orderings. J Mem Lang 11: 727–740.

Prado J, Noveck IA (2007) Overcoming perceptual features in logical reasoning: A parametric functional magnetic resonance imaging study. J Cogn Neurosci 19: 642–657.

Prado J, Chadha A, Booth JR (2011) The brain network for deductive reasoning: A quantitative meta-analysis of 28 neuroimaging studies. J Cogn Neurosci 23: 3483–3497.

Rabinowitz FM, Grant MJ, Howe ML, Walsh C (1994) Reasoning in middle childhood: A dynamic model of performance on transitive tasks. J Exp Child Psychol 58: 252–288.

Revet-ben C, Cherubini P, Frackowiak RSJ, Caltagirone C, Paulesu E, Macaluso E (2010) Conditional and syllogistic deductive tasks dissociate functionally during premise integration. Hum Brain Mapp 31: 1430–1445.

Reverberi C, Cherubini P, Rapisarda A, Rigamonti E, Caltagirone C, Frackowiak RS, Macaluso E, Paulesu E (2007) Neural basis of generation of conclusions in elementary deduction. Neuroimage 38: 752–762.

Rips LJ (1983) Cognitive processes in propositional reasoning. Psychol Rev 90: 38–71.

Smith EE, Jonides J (1999) Storage and executive processes in the frontal lobes. Science 283: 1657–1661.

Sedek G, von Hecker U (2004) Effects of subclinical depression and aging on generative reasoning about linear orders: Same or different processing limitations? J Exp Psychol Gen 133: 237–260.

Smith KH, Foos PW (1975) Effect of presentation order on the construction of linear orders. Mem Cognit 3: 614–618.

Sternberg RJ (1980) Representation and process in linear syllogistic reasoning. J Exp Psychol Gen 109: 119–115.

Stoet G, Snyder LH (2009) Neural correlates of executive control functions in the monkey. Trends Cogn Sci 13: 228–234.

Wager TD, Smith EE (2003) Neuroimaging and working memory: A meta-analysis. Cogn Affect Behav Neurosci 3: 255–274.

Waltz JA, Knowlton BJ, Holyoak KJ, Boone KB, Mishkin FS, de Menezes Santos M, Thomas CR, Miller BL (1999) A system for relational reasoning in human prefrontal cortex. Psychol Sci 10: 119–125.

Worsley KJ, Marrett S, Neelin P, Vandal AC, Friston KJ, Evans AC (1996) A unified statistical approach or determining significant signals in images of cerebral activation. Hum Brain Mapp 4: 58–73.