

available at www.sciencedirect.comwww.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****Distinct neural substrates for deductive and mathematical processing****James K. Kroger^{a,*}, Leigh E. Nystrom^b, Jonathan D. Cohen^b, Philip N. Johnson-Laird^b**^aDepartment of Psychology, New Mexico State University, 220 Science Hall, Las Cruces, NM 88003, USA^bDepartment of Psychology, Princeton University, USA

ARTICLE INFO

Article history:

Accepted 31 July 2008

Available online 15 August 2008

Keywords:

Logic

Reasoning

Math

Cortex

fMRI

Frontal pole

ABSTRACT

In an effort to clarify how deductive reasoning is accomplished, an fMRI study was performed to observe the neural substrates of logical reasoning and mathematical calculation. Participants viewed a problem statement and three premises, and then either a conclusion or a mathematical formula. They had to indicate whether the conclusion followed from the premises, or to solve the mathematical formula. Language areas of the brain (Broca's and Wernicke's area) responded as the premises and the conclusion were read, but solution of the problems was then carried out by non-language areas. Regions in right prefrontal cortex and inferior parietal lobe were more active for reasoning than for calculation, whereas regions in left prefrontal cortex and superior parietal lobe were more active for calculation than for reasoning. In reasoning, only those problems calling for a search for counterexamples to conclusions recruited right frontal pole. These results have important implications for understanding how higher cognition, including deduction, is implemented in the brain. Different sorts of thinking recruit separate neural substrates, and logical reasoning goes beyond linguistic regions of the brain.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

There have been a number of neuroimaging studies of deductive reasoning, but few have compared deduction to a comparable non-logical task. To understand what is particular to deduction, it needs to be compared to a non-logical task that also taps executive and working memory networks. There is considerable commonality of neural regions recruited by various paradigms that involve higher cognitive processing, including N-back tasks (Braver et al., 1997; Cohen et al., 1997), task switching (Dove et al., 2000; Wager et al., 2005), manipulation of working memory contents (D'Esposito et al., 1998; Petrides et al., 1993), and match-to-sample tasks (Habeck et al., 2005; Swartz et al., 1994). Frontoparietal networks are ubiquitous in studies of higher cognition (Gazzaley et al., 2004;

Buschman and Miller, 2007; Fuster, 2006; Wager and Smith, 2003). Duncan and Owen (2000), reviewing many studies attributing specific functions to localities within the frontal lobes, argued that dorsolateral prefrontal cortex is not a collection of specialized modular substrates, but is rather a unified and flexible architecture for abstract computation. Several general roles for prefrontal cortex and for widespread networks have been proposed to serve flexible information processing, including working memory and executive function (Baddeley, 2000), biasing control networks (Miller and Cohen, 2001), and supervisory control (Shallice, 1988). It would not be surprising to find that deduction depends on many of the same circuits. What is surprising, rather, is that consistent patterns of recruitment of these networks across different neuroimaging studies of deduction have not occurred.

* Corresponding author. Fax: +1 575 646 6212.

E-mail address: jkroger@nmsu.edu (J.K. Kroger).

1.1. Substrates of deduction: previous studies

Several imaging studies have examined the neural correlates of deduction, contrasting it with a baseline or other kinds of reasoning, and have reported an inconsistent assortment of neural substrates active for deductive processing. Some of these correspond to frontoparietal networks active for other higher cognitive processing but others do not. To illustrate the range of substrates reported we briefly examine several imaging studies of deduction, focusing on activation in frontal cortex. Our objective is not to build a consistent model from the findings of these studies, but rather to show that doing so is impossible by focusing on the disparity of the results. The activations in associative cortex that are recruited across all conditions in these studies, along with the manipulations evoking them, are summarized more completely in Table 1.

Studies employing very similar logical syllogisms as a deduction condition reported very different frontal lobe recruitment. Comparing deduction to a control condition, Goel and Dolan and their colleagues have observed deductive processes recruiting left inferior frontal cortex (Goel et al., 1997) and later left inferior frontal cortex with bilateral middle frontal gyrus (Goel and Dolan, 2004). Two studies contrasting logical reasoning (deduction with syllogisms) and probabilistic reasoning found left mesial frontal involvement for deduction (Osherson et al., 1998) and later right inferior and middle lateral, right medial, and left middle gyrus frontal lobe activity during deduction (Parsons and Osherson, 2001). Comparing responses to complex and simple deduction problems under the assumption that deduction substrates would be more active for complex than for simple problems, Monti et al. (2007) found bilateral and medial frontal activation superiorly, bilateral inferior frontal gyrus, and left frontopolar activation.

1.2. Deduction and spatial processing

Some researchers have employed problems built on spatial relationships in an attempt to elicit processing in spatial areas of the brain which may be substrates for mental models used in reasoning. A further motivation in these studies may have been to demonstrate that reasoning processes can occur without invoking language processing areas. Knauff et al. (2002) found bilateral middle frontal gyrus (BA 9 and BA 6) activity for both spatial relational syllogisms (“The red rectangle is to the left of the green rectangle.”) and *modus ponens* and *modus tollens* syllogisms. However, when contrasted with spatial and when contrasted with non-spatial three-term problems, Goel et al. (1998) found that left inferior and superior frontal gyri, and left middle and superior frontal gyri, respectively, were recruited by deduction. In this study, when deduction was contrasted with a non-reasoning control left inferior and middle frontal lobe was activated. The spatial and non-spatial three-term problems also recruited the same region of left frontal cortex but to a lesser extent. In another study employing relational deduction problems (Knauff et al., 2003), those with spatial content (“further south”) recruited left inferior frontal cortex and those with spatial and imageable relations (“above”) recruited left middle frontal gyrus at the inferior aspect of frontal lobe. When relational syllogisms included spatial content in these studies superior parietal lobe was more strongly recruited in the studies

by Knauff and colleagues but not in Goel et al. (1998). However, problems in the former may have invoked imagery, which recruits parietal regions (see Kosslyn et al., 2001 for a review). Knauff et al. (2002) demonstrated that visual imagery is not the same as building a mental model. Deductions that evoked images took longer for participants to make, and only they elicited activity in the parietal lobes. All the other sorts of relation, both spatial and non-spatial, evoked no such activity, suggesting that visual imagery is neither sufficient nor necessary for reasoning. Altogether, patterns of activity resulting from the interaction of deduction and spatial information have not been consistent with respect to the frontal lobe or parietal cortex.

1.3. The impact of beliefs, semantics, and emotional salience

Other studies have examined how including additional psychological elements impacts brain responses during deductive reasoning. Goel and Dolan (2003a) examined the effects of the participants’ beliefs in the conclusions, which were believable, unbelievable, or neutral. The sole effect on activity in lateral frontal regions was during trials for which beliefs elicited by problems inhibited the correct logical response. Correctly performed trials had elevated activity in right inferior frontal cortex when valid conclusions were not believable and participants inhibited the belief bias. Ventromedial frontal cortex activated when belief bias overcame logical selection of the correct answer. In another study, Goel et al. (2000) observed more activity in bilateral inferior frontal gyrus when the semantic content of an inference was not congruent with logical correctness than when it was congruent with logical correctness. When they compared reasoning with semantically correct or incorrect content to no-content reasoning (“all p are b”), bilateral inferior frontal lobe was recruited, and bilateral middle frontal activity was observed in the opposite comparison. In another study of the effects of semantic factors, when Parsons and Osherson (2001) subtracted activations from judgments about whether sentences contained semantic anomalies from activations from deductive reasoning, and when they subtracted activations from probabilistic reasoning from those for deductive reasoning, right inferior, middle lateral, and anterior medial frontal recruitment was observed.

Two additional psychological elements studied are the effect of social cognition and emotion on deductive processing. Canessa et al. (2005) imaged brain responses as participants solved four-card problems with abstract content and four-card problems that required reasoning using rules governing social interaction. Compared to a non-reasoning baseline, these tasks respectively were accompanied by left medial and superior gyrus and right middle gyrus frontal activity, and bilateral middle, superior, and medial gyrus activity. When Goel and Dolan (2003b) subtracted activation for solving syllogisms containing emotionally salient content from activation for solving neutral syllogisms, left middle frontal gyrus activity was found, and when activation during a baseline task was subtracted from activation for both kinds of syllogism, left superior frontal gyrus was also active.

In sum, there is neither a consistent picture of what the substrate for deductive reasoning is, or how it interacts with

Table 1 – Varying patterns of neural response observed in reasoning studies

Substrates of deduction		
Authors	Conditions	Findings
<i>Deduction and other sorts of reasoning</i>		
Goel et al. (1997)	<p><i>Deductive inference:</i> Subjects were asked whether the third sentence was entailed by the first two sentences</p> <p><i>Induction:</i> Subjects indicated whether a conclusion was plausible given the premises</p> <p>Control: ‘How many of the three sentences on each screen have people as their subject?’</p>	<p><i>Deductive inference minus control:</i> L Inf. Front. Gyrus (BA 45, 47)</p> <p><i>Induction minus control:</i> L Med. Front. (BA 8); L Sup. Front (BA 9); L Orb. Inf. Front. (BA 47); L Mid. Front. (BA 10); L Cing. Gyr. (BA 24,32); L Inf. Temp. (BA 20)</p> <p><i>Induction–deduction:</i> L Sup. Front. (BA 8,9)</p>
Goel and Dolan (2004)	<p><i>Deductive inference:</i> Judge the validity of syllogisms</p> <p><i>Induction:</i> Subjects indicated whether a conclusion was plausible given the premises</p> <p>Control: 3rd sentences of different syllogisms were interchanged such that the three sentences did not constitute arguments. (e.g. (1) “No reptiles are hairy; Some elephants are hairy; No pairs are green;” and (2) “Some elephants are hairy; George is an elephant; All pairs are green”</p>	<p><i>(Deductive reasoning plus inductive reasoning) minus (deductive baseline plus inductive baseline):</i> L Inf. Temp. (BA 37); Bilat. Sup. Par. (BA 7); L Inf. Par. (BA 40); R Mid. Front. (BA 6); R Med. Front. (BA 6); L Inf. Front. (BA 45)</p> <p><i>Deductive inference minus control:</i> L Inf. Temp./Occ. (BA 37/19); L Mid. Temp. (BA 39); Sup. Par. (BA 7); Bilat. Mid. Front. (BA 6); L Inf. Front. (BA 44, 45)</p> <p><i>Induction minus control:</i> Bilat. Sup. Par. (BA 7); L Inf. Par. (BA 40); R Mid. Front. (BA 6); Bilat. Med. Front. (BA 6); L Mid. Front. (BA 8,9,45)</p>
Osherson et al. (1998)	<p><i>Deduction:</i> Determine validity of syllogisms</p> <p><i>Probabilistic reasoning:</i> Determine whether (invalid) conclusion more likely to be true or false</p> <p><i>Meaning control:</i> Determine whether premises or conclusion contained anomalous content</p>	<p><i>Deduction minus meaning control (area common with probabilistic minus meaning control):</i> L Mesial Front. (BA 6)</p> <p><i>Probabilistic reasoning minus meaning control:</i> Ant. Cing. (BA 24,32)</p> <p><i>Deduction minus probabilistic:</i> R Ant. Cing. (BA 24/32); R Sup. Par. (BA 7); Bilat. Precun. (BA 7)</p> <p><i>Probabilistic minus deduction:</i> R Insula, R Mid. Front. (BA 10); R Sup. Front. (BA 11)</p> <p><i>Meaning minus both reasoning tasks:</i> L Sup. Front. (BA 9); R Inf. Front. (BA 45,47); Orb. Front. (BA 11); L Fusif. (BA 37); Bilat. Inf. and Mid. Temp. (BA 20,21); Bilat. Temp. Pole (BA 38); R Sup. Temp. (BA 22)</p>
Parsons and Osherson (2001)	<p><i>Deduction:</i> Determine validity of syllogisms</p> <p><i>Probabilistic reasoning:</i> Determine whether (invalid) conclusion more likely to be true or false</p> <p><i>Semantic control:</i> Determine whether premises or conclusion contained anomalous content</p>	<p><i>Deduction minus semantic control (area common with probabilistic minus semantic control):</i> Precun. (BA 31)</p> <p><i>Deduction minus Probabilistic reasoning (areas also active for deduction minus control):</i> R Inf. Front. (BA 44); R Mid. and Med. Front (BA 9,10); R Ant. Cing. (BA 24); L Post. Cing. (BA 31); R Mid. Temp. (BA 21); R Fusif. (BA 37); R Temp-Par. (BA 39)</p> <p><i>Probabilistic reasoning minus deduction (areas also active for deduction minus control):</i> L Inf. Front. (BA 47); L Med. Front. (BA 9); L Insula; L Post. Cing. (BA 31); L Parahip. (BA 36); L Med. Temp. (BA 35)</p>
Monti et al. (2007)	Complex deductive inferences minus simple deductive inferences. Problems with semantic content and with pseudo-words were employed.	Complex minus simple: L Front. (BA 6, 10,11(pseudo-words only)); L Med. Front. (BA 8); Bilat. Inf. Front. (BA 47); L Sup. Par. (BA 7); Inf. Par. (BA 40); Insula; results similar in second experiment, with addition of R Mid. Front. (BA 46) and Bilat. Mid. Front (BA 9) but no R BA 6 or 47.
<i>Deduction and spatial representation</i>		
Knauff et al. (2002)	<p><i>Conditional reasoning:</i> Modus pollens and modus tollens</p> <p><i>Relational reasoning:</i> E.g., “The red rectangle is to the left of the blue rectangle”</p> <p>Baseline: Fixation cross</p>	<p><i>Conditional minus baseline:</i> Bilat. Med. Suppl. Motor (BA 6); Bilat. Mid. Front. (BA 9); Cing. Gyr. (BA 32); Mid. Temp. (BA 21, 22); Bilat Inf. and Sup. Par. and Precun. (BA 40, 7)</p> <p><i>Relational reasoning minus baseline and relational reasoning minus conditional reasoning:</i> the same regions as conditional minus baseline, with magnitude differences, and overall smaller differences for the latter subtraction</p>
Goel et al. (1998)	<i>Deduction:</i> Judge the validity of conclusions in syllogisms, e.g. “Some officers are not privates”	<i>Deduction minus baseline:</i> L Inf. Front. (BA 45, 47); L Mid. Front (BA 46), L Mid. Temp. (BA 21, 22), L Sup. Temp. (BA 22), L Cing. Gyr. (BA 32, 24)

Table 1 (continued)

Substrates of deduction		
Authors	Conditions	Findings
	Spatial relational syllogisms: E.g., “Officers are standing next to generals”	Spatial minus baseline: L Inf. Front. (BA 45); L Mid. Front. (BA 46); L Cing. Gyr. (BA 32, 24); Inf. Temp. (BA 37) Relational minus baseline: L Inf. Front. (BA 45); L Mid. Front. (BA 46); L Cing. Gyr. (BA 32, 24) Spatial minus relational and relational minus spatial: none Deduction minus spatial: Bilat. Mid. Temp. (BA 21); L Inf. Front. (BA 45); L Sup. Front. (BA 8) Deduction minus relational: Mid. Temp. (BA 21); Inf. Front. (BA 45); Mid. Front. (BA 10) Relational minus deduction: L Par-Occ. Sulc. (BA 7)
	Non-spatial relational syllogisms: E.g., “Officers are heavier than generals”	
	Baseline: e.g., “How many of the three sentences on each screen have people as their subject?”	Spatial minus deduction: R Precun. (BA 31)
Knauff et al. (2003)	Visuospatial relations: That are easy to envisage visually and spatially, such as “above” and “below” Visual relations: That are easy to envisage visually but hard to envisage spatially, such as “cleaner” Spatial relations: That are difficult to envisage visually but easy to envisage spatially such as “further north” Control relations: That are hard to envisage both visually and spatially, such as “better” and “worse”	Visuospatial versus rest interval: Bilat. Sup. Par. (BA 7); L Mid. Temp. (BA 21); L Mid. Front. (BA 11) Visual versus rest interval: R Sup. Par. (BA 7); L Mid. Temp. (BA 21) R Mid. Temp. (BA 21); L Mid. Front. (BA 11); L Mid Front. (BA 9); R. Mid. Front. (BA 6) Spatial versus rest interval: Bilat. Precun. (BA 7); L Mid. Temp. (BA 21); L Inf. Front. (BA 47) Control versus rest interval: L Precun. (BA 7); R Sup. Par. (BA 7); L Mid. Temp. (BA 21)
<i>The impact of beliefs, semantics, social cognition, and emotional salience</i>		
Goel and Dolan (2003a)	Belief-laden syllogisms: e.g. “No reptiles are hairy; Some elephants are hairy; No elephants are reptiles;” content subjects could have beliefs about. These are further divided into facilitory and inhibitory trials, in which the beliefs supported or disagreed with the logical judgment Belief-neutral syllogisms: e.g. “No codes are highly complex; Some quipu are highly complex; No quipu are codes;” content subjects may not have beliefs about because they may not know the meaning of one or more key terms Baseline: Belief-laden syllogisms with 3rd sentence switched as described for Goel and Dolan (2004)	Correct belief-neutral trials minus correct belief-laden trials: Bilat. Sup. Par. (BA 7) Correct belief-laden trials minus correct belief-neutral trials: L Mid. Temp. Pole (BA 21) Inhibitory minus facilitory (and the inverse): no result Correct inhibitory minus incorrect inhibitory: R Inf. Front. (BA 45) Incorrect inhibitory minus correct inhibitory: Ventromed. Front.
Goel et al. (2000)	Contentful syllogisms: E.g., “All swans are black;” half were congruent (logical validity agreed with semantic correctness), half incongruent No-content syllogisms: E.g., “All P are B.” Baseline: Conclusions switched around among contentful problems and among no-content problems, as in Goel and Dolan (2004) Low-level baseline: All three sentences were unrelated	(Content minus no-content reasoning) minus (content baseline minus no-content baseline): Bilat. Fusif. (BA 18,19); L Sup. Par. (BA 7); L Mid. Temp. (BA 21,22); Bilat. Inf. Front. (BA 44,45) Content reasoning minus content preparation: L Mid./Sup. Temp. (BA 21,22); L Inf. Front. (BA 44,45) No-content reasoning minus preparation: Bilat. Fusif. (BA 18); L Sup. Par. (BA 7); Bilat. Inf. Front. (BA 44,45) Conjunction of (content reasoning minus content preparation) and (no-content reasoning minus no-content preparation): L Inf. Front. (BA 44), L Fusif. (BA 18); R Fusif. (BA 37) Content reasoning minus no-content reasoning: L. Mid./Sup. Temp. (BA 21,22); L Inf. Front. (BA 47) No-content minus content: Bilat. Sup. and Inf. Par. (BA 7,40); Bilat. Precentral Gyr. (BA 6); Bilat. Mid. Front. (BA 6)
Canessa et al. (2005)	Descriptive: Four-card selection task with rule in “If P, then Q” form describing arbitrary relation between two actions carried out by a hypothetical member of an unknown tribe (e.g., “If one cracks walnut shells, then he drinks pond water”) Social exchange: Four-card task with rule which described an exchange of goods proposed by Big Kiku, the head of an unknown tribe, to four members of the neighboring tribe of Nabars (e.g., “If you give me sunflower-seeds, then I give you poppy petals”)	Both tasks: L Inf. Par. (BA 39,40); Post. Front. (BA 8,9); Cing. Gyr. (BA 32); Med. Front. (BA 8,9); Sup. Front. (BA 6,8) Descriptive: Precun. (BA 7); R Ant. Mid. Front. (BA 46,10)

(continued on next page)

Table 1 (continued)

Substrates of deduction		
Authors	Conditions	Findings
	Baseline: which of four cards name objects mentioned in rule?	Social exchange: L Ant. Mid. Front. (BA 46); R Mid. Front. (BA 9); R Inf. Par. (BA 39,40)
Goel and Dolan (2003b)	Emotional syllogisms: Sentences that subjects could be expected to consider emotionally salient or charged, e.g., “All murderous people are criminals; All Nazis were murderous; Some Nazis are criminals.” Emotionally neutral syllogisms: Sentences that subjects could be expected to consider emotionally neutral, while the other half contained sentences that subjects could be expected to consider emotionally salient or charged Baseline: Syllogisms with conclusions switched among problems as in Goel and Dolan (2004)	Neutral reasoning plus emotional reasoning minus neutral baseline minus emotional baseline trials: L Mid. Temp. (BA 21,22); L Temp. Pole (BA 21,38); Med. Front. (BA 6); L Mid. Front. (BA 6); L Inf. Front. (BA 44) (Neutral reasoning minus neutral baseline) minus (emotional reasoning minus emotional baseline): L Front. (BA 44, 8) (Emotional reasoning minus emotional baseline) minus (neutral reasoning minus neutral baseline): Bilat. Ventromed. Front.; R Fusif. (BA 37)
Findings are presented in order discussed in text. Activations for sensory regions are not reported. Differences in subcortical and cerebellar activity exist but are not reported here. L = left, R = right, Bilat. = bilateral, Inf. = inferior, Sup. = superior, Ant. = anterior, Post. = posterior, Med. = medial, Mid. = middle, Orb. = orbital, Front. = frontal lobe, Temp. = temporal lobe, Par. = parietal lobe, Occ. = occipital lobe, Cing. = cingulate gyrus, Precun. = precuneus, Parahip. = parahippocampal gyrus, Fusif. = fusiform gyrus, Ventromed. = ventromedial, Gyr = gyrus.		

other psychological processes. Right and left middle frontal, medial frontal, inferior frontal, and anterior frontal, as well as superior parietal lobe, appear in many of the studies, but similar manipulations resulted in different patterns of activation of these regions. The inconsistency between results of deduction studies has been noted by other researchers (Goel, 2007; Monti et al., 2007).

1.4. The impact of experimental procedures

Methodological differences may contribute to this disparity. In many of these studies, contrasts were between different varieties of logical reasoning or between logical reasoning and logical reasoning mixed with an additional element. It is not possible to know in these cases whether some fundamental neural processing that underlies deduction occurred in both conditions and thus did not surface as a difference between them. In several studies by Goel, Dolan, and colleagues (Goel et al. 2000; Goel and Dolan, 2000, 2003a,b, 2004; Noveck et al., 2004), a control task ostensibly not calling for deduction formed a baseline to be contrasted with a deduction task. The deductive task presented a first premise, a second premise, and then a conclusion, which the participants evaluated. The baseline task was formed by switching the conclusion statements of problems so that the conclusion was obviously not a continuation of the logical argument, and when the participants realized the non-sequitur, they pressed a “no” key. Yet, it is possible that participants began processes involved in deduction after the second premise was presented and continued for about 3 s until they noticed that the conclusion had nothing to do with the premises. Thus BOLD responses in these fMRI studies to the second premise (which can take seconds to extinguish) might still have been present after the conclusion statement appeared. Its presence during these control problems may have weakened the subtraction between activity during the conclusion in the deduction and control problems and caused some regions mediating deduction to

be missed. Fangmeier et al. (2006) elegantly demonstrated that when participants reason about problems presented in a sequence of three assertions (two premises and a conclusion), neural responses to integrating the two premises began when the second premise was presented, leading to activation in frontopolar cortex. When the conclusion was presented, only more posterior parts of frontal cortex responded bilaterally. It is likely that a similar initiation of solution processing occurred at presentation of the second premise in the studies by Goel, Dolan, and colleagues.

Monti et al. (2007) required participants to perform deduction problems at two levels of difficulty. A contrast between the hard and easy problems, they reasoned, would reveal mechanisms of deduction because those mechanisms would exhibit a greater response to the hard than to the easy problems. They pointed out that other fMRI paradigms have shown increases in activity of a region with an increase in the cognitive demand of a task. We do not know yet whether neural mechanisms for logical reasoning behave in this way, and the method is bound to miss any components that do not increase in activity for more difficult problems. Other components recruited in deduction tasks might include those that have been shown to respond to demand intensity, such as working memory. Indeed, several studies not calling for deduction have shown recruitment of frontopolar cortex as working memory load increases or as the task increases in complexity (Rypma et al., 1999; Veltman et al., 2003). This activation was also observed by Monti et al. (2007). Thus it is not clear that a contrast between difficult and easy deduction problems will find mechanisms whose operation is the same for all deductions. Most higher cognitive tasks for which parametric increases in neural response are found involve demands to maintain or manipulate more information. So it is also not clear whether the results found by Monti et al. reflect deduction or working memory demands.

1.5. A design to evaluate competing theories

Our aim is to isolate the neural computation underlying deduction and distinguish it as much as possible from general executive functioning. This requires a control condition including computations that depend on executive processes but that does not involve deduction. The purpose of this study is to compare such a task to logical deduction. Mathematical computation is a task that should recruit regions generally subserving higher cognition, executive processing, and working memory but lacks logical processing demands, so that contrasting it with deduction should reveal any neural processing unique to deductive computation. Furthermore, researchers have carried out extensive research on the neural mechanisms underlying mathematical cognition (Dehaene et al., 1999, 2003; Lee, 2000; Simon et al., 2004), and it can serve as a reference task for the present study.

Is there any point to observing neural activation during deduction? Despite the generality of association area recruitment across different higher cognitive tasks, some broad conclusions about specialization have received convincing support. Among them, language is widely recognized to depend on left perisylvian cortex, including Broca's and Wernicke's areas (Mazoyer et al., 1993; Peterson et al., 1989; Price, 2000; Stromsworld, 1996). Processing of spatial information depends on the dorsal processing stream (Husain and Nachev, 2007; Ungerleider and Haxby, 1994) and is more likely to occur in the right hemisphere than the left (Kosslyn, 1994), including the frontal lobes, especially for representation of spatially related elements (Slotnick and Moo, 2006). Visual imagery appears to recruit visual perceptual areas in occipital cortex as well as inferior and superior parietal regions (for a review see Kosslyn et al., 2001). If deductive reasoning recruits substrates with established function that are not equally recruited in a demanding, non-logical task, conclusions can be drawn about the neural substrate of deduction. Thus the present study is designed to optimize the possibility of observing neural processing specific to deduction that might resolve theoretical questions about how humans reason deductively.

Much of the study of deductive reasoning has been motivated by two theoretical perspectives. Reasoners might apply *rules of inference* to the logical form of natural language sentences in order to derive proofs of conclusions. Because such rules operate in a formal syntactic way (Braine and O'Brien, 1998; Rips, 1994), reasoning should depend on brain regions associated with syntactic processing (Wharton and Grafman, 1998). Alternatively, logical reasoning could go beyond language: reasoners construct non-linguistic representations of the situations described in the premises, draw conclusions from these *mental models*, and establish validity by determining that the conclusion holds in all the models of the premises (Johnson-Laird and Byrne, 1991; Neth and Johnson-Laird, 1999; Johnson-Laird et al., 2000). Both the formal rule and the mental model theories have behavioral evidence in their support. Processing in language areas, as well as in non-linguistic areas, are then of particular importance to this theoretical dilemma. The present study accordingly aimed to answer the question: will observed patterns of neural activity indicate that logical reasoning depends solely on linguistic processes or that it goes beyond them and non-linguistic manipulations are essential to deduction?

The study used logical problems, such as:

There are five students in a room.

Three or more of these students are joggers.

Three or more of these students are writers.

Three or more of these students are dancers.

Does it follow that at least one of the writers in the room is a student?

Formal rule theories (Rips, 1994; Braine and O'Brien, 1998) have yet to be formulated to deal with numerical premises, but in principle reasoners could derive the putative conclusion from the premises in a series of steps, each based on a rule of inference. Alternatively, they could proceed by envisaging a model of the third premise (about writers), in which each column in the following diagram of a mental model denotes one of the five students:

Student 1	Student 2	Student 3	Student 4	Student 5
Writer	Writer	Writer		

The correct answer (yes) can be directly read off from this model. But, such immediate inferences do not readily yield empirical predictions, either behavioral or neural, that discriminate between rule and model theories. Both sorts of theory postulate that the major step is to understand a premise (the third one in the preceding example) — in one case to extract its logical form, and in the other case to construct a mental model based on its meaning. In contrast, consider the following putative conclusion from the premises above:

Does it follow that at least one of the students in the room is all three: a jogger, a writer, and a dancer?

Current rule theories propose that reasoners search through the "space" of all possible formal derivations from the premises (Rips, 1994; Braine and O'Brien, 1998). They fail to find a proof of the conclusion, and so should respond: No. In this case, logical reasoning calls for syntactic manipulations based on formal rules, and, as many investigators have suggested, it should depend on language areas of the brain in left hemisphere (Paulesu et al., 1993; Price et al., 1996; Inui et al., 1998; Ni et al., 2000; Price, 2000). Rips, for example, has suggested that rule-based deduction may operate by sentential processing: "The central notion in the theory [i.e. Rips's theory] will be that of mental proof. I assume that when people confront a problem that calls for deduction they attempt to solve it by generating in working memory a set of sentences linking the premises or givens of the problem to the conclusion or solution. Each link in this network embodies an inference rule..." The operation of these inference rules, as Rips makes clear (see e.g. his Table 4.1), is entirely syntactical (Rips, 1994).

In contrast, the model theory proposes that reasoners can establish the invalidity of the inference by constructing a counterexample, that is, a model that satisfies the premises but that refutes the conclusion, such as:

1	2	3	4	5
Jogger	Jogger	Jogger		
Writer	Writer		Writer	
		Dancer	Dancer	Dancer

Table 2 – Examples of the four sorts of problem

Prestatement	There are five students in a room.
Premises	Three or more of these students are joggers. Three or more of these students are writers. Three or more of these students are dancers.
Easy logic (yes)	Does it follow that at least one of the writers in the room is a student?
Hard logic (no)	Does it follow that at least one of the students in the room is all three: a jogger, a writer, and a dancer?
Easy calculation (yes)	X equals the minimum number of joggers in the room. $(X+24) + (X-1) = 29?$
Hard calculation (no)	X equals the number of students in the room. $((12+3X) * X/5) * X = 150?$

Two easy and five hard logical problems analogous to those in Johnson-Laird and Hasson (2003) served as the basis for the ten easy and ten hard logical problems used in this study. The base versions were varied using three different numbers of persons in the room, different occupations and avocations, and logically equivalent different formulations in the questions (e.g. “one or more” to “at least one”). The math problems used twenty different equations selected from the pilot study. The result was 40 distinct problems. A careful debriefing of the participants revealed that they had not detected the similarity in form across problems. The correct answers are shown in parentheses.

In this case, logical reasoning should go beyond linguistic regions in the brain and may activate regions implicated in spatial representation, as reasoning processes form and manipulate arrangements of problem elements (Johnson-Laird, 1995). Behavioral studies have shown that individuals do construct counterexamples (e.g. Neth and Johnson-Laird, 1999). Individuals do not invariably search for counterexamples, and so some theorists have proposed model based theories in which they play no role (e.g., Polk and Newell, 1995). More recent evidence, however, implies that an optimal way to elicit a counterexample is to present a conclusion for evaluation that is consistent with the premises but that does not follow of necessity from them (Johnson-Laird and Hasson, 2003). Given paper and pencil, they draw diagrams akin to the

Table 3 – Reaction time and error rates

	Easy	Hard
Logical problems	6870 (2)	10,513 (29)
Mathematical problems	7633 (19)	11,747 (18)

The mean latencies (in ms) for responding correctly to the four sorts of problem, and the percentages of errors (in parentheses). There were no significant differences between the logical and mathematical problems in latencies or errors (ANOVA: $F(1,15)=4.1710$, $p>.05$, and $F(1,15)=3.2806$, $p>.05$), though the hard problems in both cases took longer than the easy problems. The interaction between the type of problem and the level of difficulty was significant for the accuracy data ($F(1,15)=36.5743$, $MSE=82.71$, $p<.0001$). However, this pattern is not observed in the neuroimaging results. For the ROIs where activation differed for logic and math (Fig. 2), the easy logic problems elicited activation similar to the activation for hard logic problems, and both differed significantly from the activity for mathematical problems. In frontal pole, activation during easy and hard math problems was comparable to that for easy logic problems, remaining at roughly baseline activation level.

preceding one. Every participant engaged in constructing counterexamples, but they sometimes erred when they failed to find one. Neuroimaging studies have examined logical and inductive reasoning, but have not examined the potential search for counterexamples.

The logical and mathematical problems used information from the same premises. For example, the premises above can be combined with the following question:

X equals the number of students in the room. $(X+24) + (X-1) = 29?$ Half the logical and mathematical problems were easy and half were difficult. The easy logical problems were immediate inferences from the premises, whereas the hard logical problems called for a search for counterexamples (see Table 2). The easy mathematical problems called for simple mental calculations, and the hard mathematical problems called for more complex calculations from longer formulas. Both the easy and the hard logical and mathematical problems were matched for mean solution times at each level of difficulty. Fig. 1 presents the design of the fMRI study and the timing of the events on each trial.

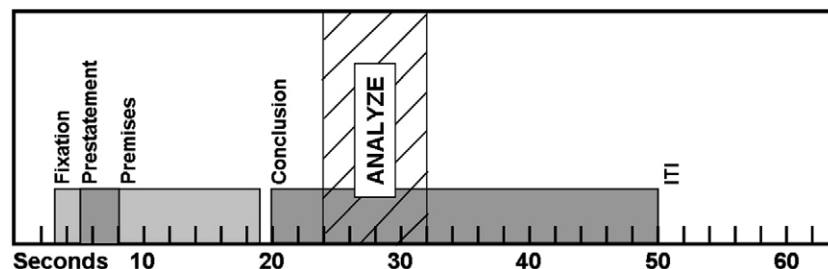


Fig. 1 – The timing of events in a trial. The prestatement remained onscreen while the premises were presented; both were removed 1 s prior to presentation of the problem statement (the conclusion for logic or the equation for math). Appropriate epoch durations were determined from the non-speeded pilot study, which showed also that mean response times were the same for both the logical and mathematical problems used here (at the easy and hard levels, respectively). Analysis was performed on data collected during the hash-marked window, to capture activity beginning when the conclusion was presented, adjusted for a 4-second hemodynamic lag.

2. Results

2.1. Behavioral results

We carried out analyses of variance for two factors: the type of problem (logic versus math) and the difficulty of the problem (easy versus hard) on both response times (from the presentation of a conclusion or formula to the response) and accuracy. Table 3 presents the mean latencies of the responses and the percentages of errors for the four sorts of problem.

Overall, responses to hard problems were significantly longer than to easy problems ($F(1,15)=34.44$, $MSE=6,989,795$, $p<.0001$), and they were significantly less accurate ($F(1,60)=30.23$, $MSE=82.71$, $p<.0001$). There was a trend for math problems to take longer than logic problems, but the difference was not significant ($F(1,15)=3.81$, $MSE=4,186,776$, $p>.05$), nor was there significant difference in accuracy ($F(1,15)=1.89$, $MSE=82.71$, $p>.05$). There was no reliable interaction between the type of problem and its difficulty for response times ($F(1,15)=.19$, $MSE=4,763,330$, $p>.05$). But, for accuracy, these two variables did interact ($F(1,15)=36.57$, $MSE=82.71$, $p<.0001$): the easy logic problems tended to yield more accurate responses than the hard logic problems, whereas accuracy on the easy and hard math problems was almost the same. The hard logic problems were indeed more difficult than either sort of math problem, presumably because of the relative difficulty of searching for counterexamples.

2.2. Bold results: main effects of problem type and difficulty

A network of regions responded significantly more while processing the logical problems than during the math problems ($p<.0001$). Their locations and the time course of their activations are depicted in yellow/red in Fig. 2 and the locations of the ROIs are listed in Table 4. Regions that responded significantly more during mathematical problems ($p<.0001$) and their time courses are depicted in blue. Statistical analysis was performed on the 8-second period after presentation of the conclusion by focusing on a period from 4 to 12 s after the conclusion appeared. This 4-second shift accommodated hemodynamic lag, and is represented by the cross-hatched region in Fig. 1 and the vertical gray bar in each time course plot in Fig. 2. Responses to reading the problem statement and premises are apparent to the left of this bar.

The network of regions engaged following appearance of the conclusion in the logic problems include perisylvian language areas (Broca's area, left Brodmann's areas 44 and 45; Wernicke's area, left BA 41 and 42), inferior parietal lobule bilaterally (BA 39 and 40), and in frontal cortex, and several additional regions in right frontal cortex (BA 8, 9, 44, and 45). A precentral gyrus activation occurred near the left hemisphere hand control area (BA 4). Areas responding during solution of the math problems include a frontoparietal network including left prefrontal cortex (BA 9/46), bilateral caudate, and bilateral intraparietal sulcus (BA 7). Additionally, bilateral frontal eye fields were recruited (BA 8).

It is clear in the time course plots that most of these regions were selectively recruited by the logic or math task, and it is

not the case that they tended to participate in both tasks, but to a different degree. Furthermore, in inferior parietal cortex (BA 40) and Wernicke's area (BA 42), a marked suppression of activity is apparent during math processing.

No significant activations were observed for the level of difficulty main effect at $p<.0001$, but the .0005 threshold revealed four significant regions of interest (ROIs). A planned comparison revealed that all four comprised greater activation for hard than for easy problems ($p<.0005$). One of the ROIs was in prefrontal cortex on the lateral surface of the right hemisphere (BA 46). The other three ROIs were in left precentral and postcentral gyri and in left posterior cingulate.

2.3. Isolating activity for deductive calculation

This study aspired to resolve a conflict between two theoretical perspectives on human deductive reasoning: whether mental models or syntactic rule processing underlies deduction. The neural engagement reported so far does not point to a resolution of this debate. Both language areas and right frontal cortex appear to participate during the deduction problems, suggesting both syntactic and visuospatial computation. To test this conclusion, we exploited two findings: 1) the hard logic problems took considerably longer to solve than the easy logic problems — 10,513 and 6870 ms, respectively; 2) results of the ANOVA indicated that the intensity of activity during the 8-second analysis window did not differ significantly in these regions for hard and easy logic problems. But in the period following the 8-second window, there should be more protracted processing of the hard problems, as evidenced by the reaction times. Thus, by performing an analysis that considered the entire 30-second solution period, rather than the 8-second window, differences between the total neural activity for hard and for easy problems over the entire solution time should be detectable. These are likely to reflect differences in the duration of computation, rather than differences in intensity of neural activity for the easy and hard problems. Thus, voxels exhibiting this difference must be where parsing the logic problems occurs. A mask was used to limit analysis to the voxels that were more significantly activated during logic than during math problems. A separate t-test analysis was performed over the entire 30-second response period for those voxels (Fig. 3). Most voxels in the right BA 8/9 (75%) and right medial BA 8 (56%) ROIs were significantly more active for the hard than for the easy problems ($p<.005$) during this response period (Fig. 4). A minority of voxels scattered bilaterally through the ROIs in bilateral BA 40 (21%) were also significant ($p<.005$). Peak intensities were similar for hard and easy problems, and none of these voxels were significant either in the main effect for difficulty or in the interaction between difficulty and the type of problem. We therefore conclude that the significantly greater activation over the solution period is a result of a longer activation for the hard problems than for the easy problems and that the green-colored voxels in Fig. 4 represent the regions engaged in logical calculation. These voxels are primarily in right prefrontal cortex. As Fig. 2 shows, this tendency occurs in the time course of activations for the more anterior right and medial frontal lobe ROIs (BA 8, 8/9). No language-associated regions or other brain

areas exhibited this difference in the duration of activity for hard and easy problems.

2.4. Response to complex deduction problems

There was an interaction between the type of problem and level of difficulty for an ROI in right frontal pole (BA 10). The

interaction was significant ($p < .005$), but none of the planned comparisons were significant. This anterior region of the head is highly susceptible to motion artifact, and examination of the data revealed spuriously large and rapid changes in signal uncorrelated with trial events owing to head movements in four participants. Their data were excluded. The interaction between the type of problem and level of difficulty remained

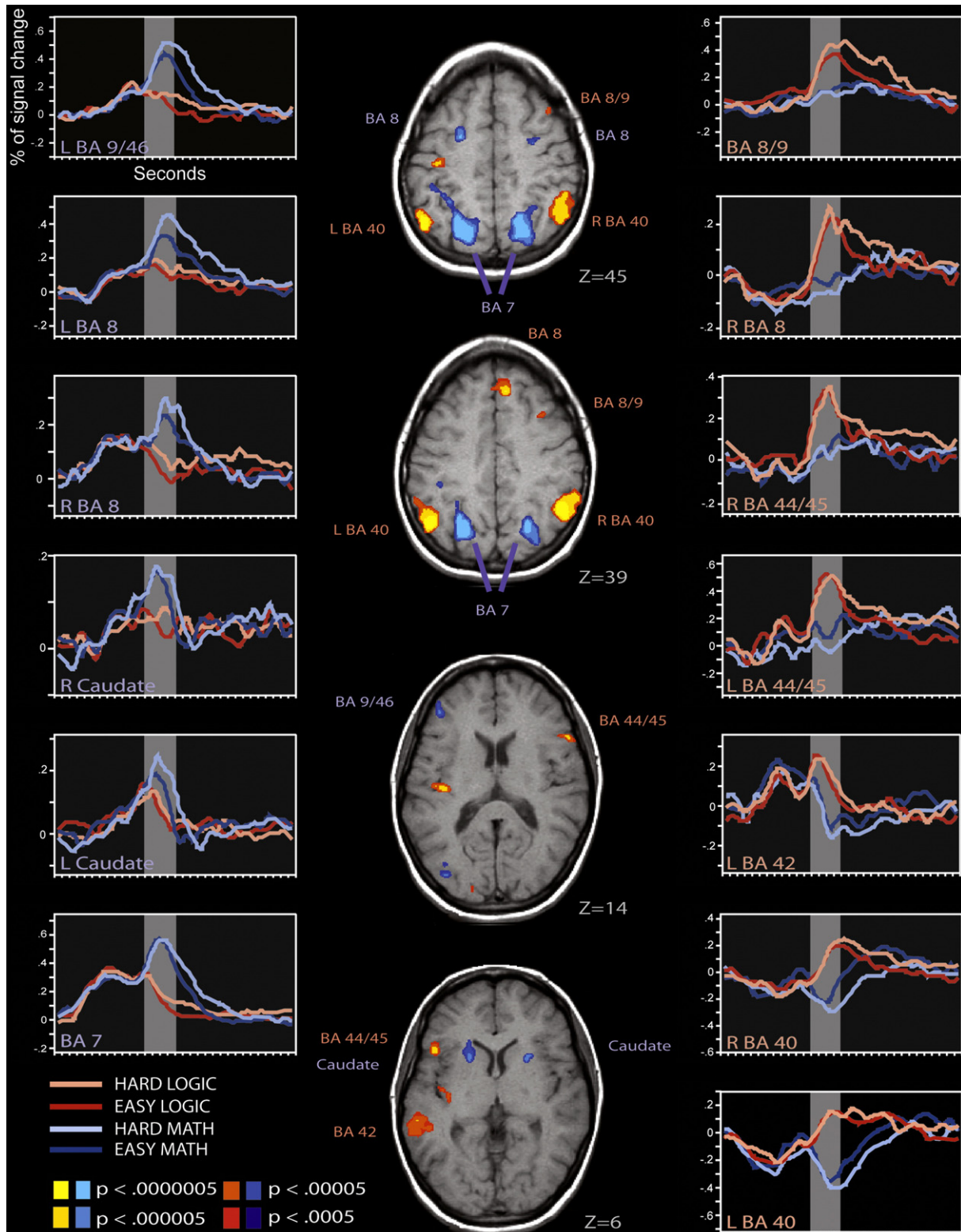


Table 4 – ROIs observed in the contrast between logic and math problems

Region (BA)	Hemisphere	x	y	z	# Voxels	Max z
<i>Type of problem</i>						
MFG (8)	R	37	21	39	8	4.15
IPL (40)	R	–51	–61	44	143	5.62
MFG (8/9)	R	8	42	34	51	5.04
MFG (8)	L	–24	5	47	10	–4.77
MFG (8)	R	28	0	47	6	–4.79
PrCG (4)	L	–37	–16	47	19	4.75
IPS (7)	B	–21	–67	50	442	–6.24
MFG (9/46)	L	–40	40	25	32	–4.58
IPL (40)	L	–51	–53	42	96	5.93
PoCG (43)	L	–46	–17	23	46	4.76
IFG (45)	R	56	26	13	6	4.65
Caudate	L	–20	15	8	18	–4.81
IFG (44/45)	L	–39	22	–5	64	4.97
Caudate	R	18	16	–7	9	–4.51
STG (42)	L	–60	–26	10	37	4.69
MOG (18)	L	–20	–92	22	12	4.64
<i>Level of difficulty</i>						
PrCG (4)	L	–37	–13	50	9	4.33
MFG (46)	R	45	35	24	10	4.13
PC (31)	L	–2	–37	29	9	3.49
PoCG (43)	L	–47	–16	19	10	3.78
<i>Type × difficulty interaction</i>						
SPL (7)	R	32	–55	54	33	1.75
SPL (7)	L	–32	–55	54	19	1.85
STG (22)	R	48	–29	9	7	2.01
SFG (10)	R	30	63	–1	8	2.62

Regions of interest (Brodmann's areas, BA), hemisphere, Talairach coordinates of most significant voxel (x, y, and z), the number of voxels, and the maximum value of z (on the normal distribution). The ROIs are the foci of significant activation differences as a function of the type of problem (logical or mathematical), its level of difficulty (easy or hard), or their interaction. SFG = superior frontal gyrus, MFG = middle frontal gyrus, IFG = inferior frontal gyrus, IPL = inferior parietal lobule, PrCG = precentral gyrus, IPS = precuneus, PoCG = postcentral gyrus, STG = superior temporal gyrus, MOG = middle occipital gyrus, PC = posterior cingulate, SPL = superior parietal lobule.

significant for the 12 remaining participants ($p < .005$) and all the significant ROIs remained the same for them. A planned comparison revealed that during the 8-second window, the hard logical problems activated this region more than the easy logical problems did ($p < .025$). Behavioral results reveal that the hard math problems were more difficult than the easy math problems, but there was no significant difference in their recruitment of frontal pole ($p > .05$) and only the hard logic

problems showed elevation above baseline there. The peak of activation for hard logic problems occurred several seconds after participants began solving the problems. Interestingly, this time course is similar to the right frontal regions revealed by analyzing the full solution period. We interpret this phenomenon as a high-level manipulation of mental models after they have been constructed.

2.5. Analysis for common processing

We also addressed the question of what brain regions might be participating for solution of both the logic and the math problems. One approach to such a question is a conjunction analysis, in which a control condition is subtracted from each of two experimental conditions, and the intersection of the two differences is taken. The present study did not include a control condition, precluding execution of a conjunction analysis. We explored a different approach to determining recruitment common to both tasks: subtracting easy logic from hard logic, and easy math from hard math, and computing the intersection between the two differences. No significantly different activations for easy and hard math were found ($p > .05$), so no intersection was calculated. This is in accord with the similar levels of activation intensity observed for easy and hard problems; this is considered further in the discussion.

3. Discussion

3.1. The substrate for deduction

Fig. 2 presents the regions of the brain yielding reliable differences between logical reasoning and mathematical calculation (regions significant at $p < .0001$). A frontoparietal network including right prefrontal cortex, perisylvian language areas, bilateral inferior parietal lobule, and middle occipital gyrus were significantly more active during the deduction problems. Spatial processing has been associated with the right hemisphere (Baddeley, 1996; Kosslyn, 1994; Slotnick and Moo, 2006; Smith et al., 1996). This activation is consistent with executive processing of spatial information.

3.2. The role of language areas in deduction

Broca's and Wernicke's regions and right inferior frontal cortex responded more during the logic than the math problems, and, as may be seen in Fig. 2, the left-hemisphere language areas were active as the premises were read. It appears that soon after

Fig. 2 – The differences between logical reasoning and mathematical calculation in brain activity. Red and yellow indicate regions in which reasoning yielded reliably more activity than calculation, and shades of blue indicate regions in which calculation yielded reliably more activity than reasoning. The figure also presents the timelines for the easy and hard problems of both sorts. The analysis was conducted on the 8-second period indicated by the gray bar. The ROI anterior to Brodmann's area 42 extends inferiorly into area 42. A left hemisphere ROI apparent at $z = 45$ is in the motor region for hand control (participants responded with their right hand). Logical processing elicited primarily right prefrontal activation, while activation accompanying mathematical processing occurred in the left frontal lobe. The exception was bilateral frontal eye field (BA 8), which typically mediates eye movements, and was highly active during mathematical calculation, presumably as a result of foveation of the equation throughout its solution.

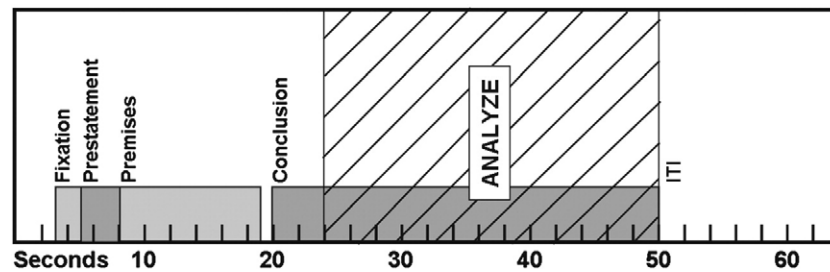


Fig. 3 – A mask selected ROIs more active during logic than during math problems. To discriminate regions active throughout the solution of deductive problems, activation in these ROIs was compared for hard and easy logic problems during the full solution epoch (hash-marked window, adjusted for 4-second hemodynamic lag).

the presentation of the conclusion, these regions exhibited a peak in activation that was short in duration relative to activity in right frontal cortex, then quickly returned towards baseline. This pattern indicates that linguistic processing occurred for the conclusion to complete an understanding of the problem, but then it ceased and processing shifted to the construction of a visuospatial representation mediated in right frontal cortex. This conclusion is confirmed by our comparison of reasoning activity for hard and easy logic problems during the entire solution period. None of the language areas remained significantly active as the solutions were computed. Recruitment of left visual cortex (Brodmann's area 18) may also have resulted from processing of a visuospatial representation, but this activity did not differ significantly between hard and easy logic problems during analysis of the 30-second solution window.

Difficulties may arise when linguistic processing is equated with logical processing. As is evident from the time courses in Fig. 2, solution of the deduction problems could not have occurred without the preceding linguistic processing. The interpretation of a problem that is presented linguistically must occur before mental models can be constructed. Monti et al. (2007) also observed this sequence of activation first in language areas and then in other cortical regions. Thus, we should be cautious in explaining diminished reasoning abilities in patients with compromised left frontal cortex to a loss of the reasoning substrate (Adolphs et al., 1996; Goel et al., 2007; Varley and Siegal, 2000). The deficit could simply be because, when presented with a problem, the patients are unable to comprehend it or to form a representation of it. In the case of studies with split-brain patients (Gazzaniga, 1985; Gazzaniga and Smylie, 1984), these patients may be able to form a linguistic representation, but be unable to construct a right-hemisphere model of it.

3.3. Frontopolar cortex and complex deduction

In our study, anterior prefrontal cortex, or frontopolar cortex, is the sole locus specializing in the harder logic problems. This region differs from more posterior cortex in several respects. Pyramidal neurons there are sparser but have richer, more complex dendritic trees which receive more inputs than other association areas and their intracortical connections are primarily to other supramodal association cortex (Jacobs et al., 2001; Travis and Jacobs, 2003). This morphology suggests a role of integrating function or representations across the higher

processing centers in the brain. It is the most recently evolved part of the frontal lobes (Semendeferi et al., 2001) and is a late cortical structure to reach maturation (Flechsig, 1901; Gogtay et al. 2004), which can be delayed by years as a function of measured intelligence (Shaw et al., 2006). We surmise that the more complex models required by these problems called for assembling and reordering structured representations in which logical validity depended on relations among model elements. This interpretation is consistent with findings that relational complexity (Robin and Holyoak, 1995; Halford et al. 1998; Holyoak and Thagard, 1995) demands executive processing capacity (Halford et al., 1998; Kroger and Holyoak, 2004) and depends on frontal cortex. It is degraded in aging, in Alzheimer's patients (Waltz et al., 2004), and when the integrity of frontal cortex is compromised (Waltz et al., 1999). The solution of problems high in relational complexity recruits frontopolar cortex (Kroger et al., 2002). It is because of the relational complexity of models used for the hard logic problem that they depended on frontopolar cortex.

3.4. Substrate for mathematical processing

A different frontoparietal network responded most to mathematical processing that included left dorsolateral frontal cortex, bilateral superior frontal cortex comprising the frontal eye fields, bilateral caudate, and bilateral superior cortex. The language areas did not show so large a response when the formula was presented as they did when the logic conclusion was presented. This difference might be because participants continued to look at the formula in order to solve it piecemeal, rather than comprehend the formula in its entirety, as they did for the logic conclusions. But, it might also be because reading and interpreting the formulas did not depend on language areas. The pattern of neural responses while solving the formulas is consistent with responses to mathematical processing observed by Simon et al. (2004): the activation primarily of a left frontoparietal network involving bilateral superior parietal lobule. Superior parietal cortex, part of the dorsal route for visual information processing, mediates spatial information (Dehaene et al., 2003). Dehaene et al. argue that since numerical values may be represented as a number line with spatial dimension, this region contributes magnitude judgment to mathematical thinking.

Our finding of left dorsolateral frontal activation in conjunction with caudate is consistent with other studies of

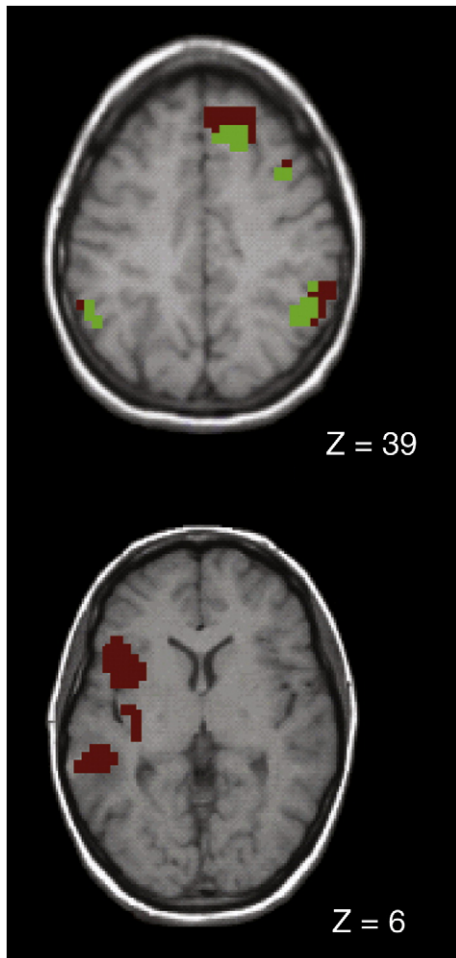


Fig. 4 – Red regions (including the left hemisphere language areas) are ROIs which were more active during logic than during math problems, but whose average activity over the whole 30-second solution window was not different for hard and easy logic problems, despite the longer time participants spent solving the hard problems. Green regions (including right frontal activations and bilateral inferior parietal activations) are areas that were more active over that period for hard problems than for easy problems, so were active for a time corresponding to the time required for solution. ROIs in middle occipital gyrus, and precentral sulcus that were more active for logic than for math are not depicted, and were not significantly different in this analysis.

mathematical processing (Dehaene et al., 1999, 2003; Simon et al., 2002, 2004). The cortex is anatomically connected to the basal ganglia through a series of parallel bidirectional loops. Dorsolateral prefrontal cortex shares relatively greater connectivity with the caudate head, and evidence suggests that the caudate head may be more sensitive to executive processing (Melrose et al., 2007). Working memory is necessary for encoding, maintaining, and performing calculations with the numbers in the math conclusions. Thus activity

there is consistent with earlier work and reflects the interaction of left dorsolateral cortex with caudate during this processing.

Dehaene et al. (2003) and others have observed inferior parietal participation in mathematical computation, but our results are not in agreement with this observation. We observed significant engagement of inferior parietal cortex by deduction, but not by the solution of the math problems. The significance of the comparison between them is partly due to the suppression of activity there during the math problems. The BOLD response for math is suppressed roughly twice as much for math as it is elevated for logic in left BA 40, and the two are roughly equal in right BA 40. The maxima of these ROIs are superior to Brodmann's area 40 (supramarginal gyrus), near its junction with area 39 (angular gyrus). This finding is contrary to views about the association between mathematical processing and inferior parietal lobule, which have a history dating back to Gerstmann (1924). He observed a cluster of deficits resulting from damage to angular gyrus, including acalculia. Neuroimaging studies of calculation have frequently revealed angular gyrus involvement in calculation (Dehaene et al., 1999; Grabner et al., 2007; Menon et al., 2000) and less often, supramarginal gyrus (Simon et al., 2002; Dehaene et al., 2003; Fehr et al., 2007). Dehaene et al. (2003) credit this recruitment in angular gyrus to verbal mediation of numbers in calculation in keeping with its association with phonological processing. They suggest that subtraction and addition call for magnitude judgment and depend on superior parietal cortex whereas multiplication and division require use of rules. Lee (2000) has also found evidence for this anatomical dichotomy. Mediation of the mathematical rules would depend on phonological and semantic representation of numbers and thus engage angular gyrus (Dehaene et al., 2003).

Inconsistent findings have clouded the exact role of the inferior parietal lobule in calculation. van Harskamp et al. (2005) observed intact supramarginal and angular gyri in a lesion patient who lost ability to retrieve multiplication facts but not addition facts, and preserved multiplication ability in another patient with lesions in supramarginal and angular gyrus. Mayer et al. (1999) reviewed the literature on the Gerstmann syndrome, and noted that a range of divergent number-related deficits are credited to the syndrome, from inability to calculate to inability to count. They examine in detail a case of pure Gerstmann syndrome caused by focal damage to white matter underlying angular gyrus, and conclude that the underlying defect is in the ability to manipulate images. This conclusion is consistent with other findings regarding visual or spatial imagery and inferior parietal lobe: Brunetti et al. (2007) observed supramarginal mediation of identification of the location of an auditory target, Krueger et al. (2007) found angular and supramarginal gyrus responses to selection of a spatial target, more so in the right hemisphere, and in a study by Yeh et al. (2007) inferior parietal lobule activity was key to directing attention to change detection for spatial and color features. Caplan et al. (2006) also observed more activity in the right inferior parietal lobule for attention to motion. Using fingers to imitate novel actions (Tanaka et al., 2001), construction of an object shape with hand motion (Jancke et al., 2001), and attention to limb movement (Rushworth et al., 2001) recruit supramarginal gyrus.

Gerstmann syndrome is also characterized by disruption of spatial discrimination as well as finger agnosia, and inferior parietal cortex plays a role in spatial working memory (Leung et al., 2007; Olesen et al., 2007; Olesen et al., 2003; for a review see Vallar, 2007). Given the participation of right hemisphere but not perisylvian language areas during the deduction problems and greater inferior parietal activity in right hemisphere, it is likely that the latter results from manipulation of mental models in visuospatial working memory. That the region is suppressed for math processing when participants have the formula before them and can consult it in stepwise manner, but active for deduction, further supports this argument.

Bilateral activation in BA 8 corresponds to the frontal eye fields; this may result from participants shifting their gaze among parts of the mathematical equation, whereas it was not necessary to keep gaze as steadily fixed on the logic conclusion. Frontal eye fields are associated with control of gaze (Berman et al., 1999) and with directing visual attention (Corbetta et al., 1998).

3.5. Difficulty of the two problem types

Our attempt to perform a conjunction analysis revealed no significant difference in the neural substrates recruited for easy and hard math problems. We elected to match our math and logic problems on reaction time as a way to equate difficulty across the problem types and to keep solution and fMRI sample times comparable across conditions. We observed a difference in accuracy for the easy and hard logic problems but not for the easy and hard math problems. Taken together this suggests a larger qualitative difference between processing of the easy and hard logic problems than between the easy and hard math problems. It may be that while the search for counterexamples in the hard logic problems entailed qualitatively different processing from solution of the easy logic problems, essentially the same processing was required for solving all math problems but it lasted longer for the hard math problems. These results seem consistent with findings of similar neural processing substrates in various studies of mathematical processing (Dehaene et al., 1999; Simon et al., 2002). A future study would benefit from inclusion of a baseline control condition which could be subtracted from the logic and the math conditions, to permit better observation of the intersection between the neural substrates recruited by them.

3.6. Comparison with previous findings

In contrast to some other studies, we found no left frontal activation during solution of the deduction problems, except in Broca's area. Activity here has been implicated in verbal tasks and may reflect subvocal processing of verbal information (Gruber et al., 2001; Henson et al., 2000; Smith et al., 1998). This region has also been implicated in semantic retrieval (Sabb et al. 2007) and in selection among competing perceptual or semantic possibilities, such as when a sentence completion or verb generation task has many possible answers (Thompson-Schill et al. 1997). In deduction studies employing paradigms where participants aborted processing of control problems when a conclusion was

unrelated to the premises (Goel et al. 2000, Goel and Dolan, 2000, 2003a,b, 2004; Noveck et al., 2004) subvocalization would cease, and subtraction of activity during the baseline period during which no conclusion was being computed from the same conclusion period in deduction problems could then explain recruitment of this region as subvocalization. Similarly, when reasoning involved semantic content, regions responsible for semantic processing would appear if activity during solution was contrasted with activity when solution was aborted. This subtraction could produce a left ventral frontal ROI. The same is true for selection. Any of these processes in inferior frontal cortex could account for the fact that inferior left frontal activations appear in several studies using this sort of baseline task. Even if we disregard these alternate explanations, activation in left inferior frontal cortex during deduction does not necessarily mean that it participates in deductive reasoning, as is demonstrated by the results of the present study. We observed activations in Broca's region during encoding of the premises and conclusion which were not sustained during solution of the deduction problems.

Response intensity of the ROIs we observed in right frontal cortex did not differ in intensity. If similar regions were active in the study performed by Monti et al. (2007), they would not have been detected, since the regions they attribute deduction to were found by a contrast between their complex and simple deduction problems. Moreover, the activations they found are not a result of differing durations of processing, as in our 30-second window analysis, since they focused on shorter windows of equivalent duration for the complex and simple problems. These issues may explain why Monti et al. failed to find right frontal activation for deduction, and emphasize the difficulty of elucidating the neural substrate of deduction from a paradigm in which both conditions in a contrast depend on logical reasoning.

3.7. Conclusion

The present results seem incompatible with a purely linguistic theory of logical reasoning, which employs only formal rules of inference operating on the logical form of sentences. One indication to the contrary is in the participants' reports in the pilot study on how they tackled the logical problems: they used their fingers or envisaged spatial models to represent the potential overlaps among the individuals in the room. Such a process is hard to reconcile with the use of purely formal rules. The rule theories postulate a search for a formal derivation for both easy and hard problems, which differ only in the number of premises that need to be taken into account. And so another difficulty for the theory is to explain why linguistic processes in reasoning should activate *right* prefrontal cortex. No current formulation of rule-based reasoning postulates mechanisms that should recruit this region, and some authors have claimed that deduction depends only on left prefrontal cortex. Wharton and Grafman wrote: "Reasoning about highly imageable, content-independent situations appears to be mediated by left posterior regions rather than by the right hemisphere. This finding appears to weaken deductive reasoning theories based on non-verbal cognition." They conclude: "mental model theory's claim of a mostly non-verbal deductive reasoning

process does not appear to be borne out by initial clinical and neuroimaging data" (Wharton and Grafman, 1998, p 58).

How are we to make sense of the results? It is necessary to speculate, but our account is constrained by our computational implementation of the model theory, the behavioral evidence on the search for counterexamples, and existing knowledge of neural functions. The participants have to read the premises, and at that point they cannot tell whether the problem will be logical or mathematical. They soon became practiced and reported that they usually extracted and encoded the numbers and the different sorts of individuals referred to in the premises. There is a concomitant pattern of three components in brain activity during this period of reading the premises: a brief elevation of language areas; sustained elevation in the frontal and inferior parietal areas mediating working memory; and suppression in some frontal and posterior areas. For the logical problems, reasoners must then understand the question posed by the conclusion. This process also recruits language areas. The question can be answered either immediately from the model of a single premise (the easy problems) or from a search for counterexamples (the hard problems). Reasoners could, of course, search for counterexamples to the conclusions of easy problems. However, their initial models of the premises yield the correct answer in any case, whereas their initial models for the difficult problems represent all three premises and may yield the wrong conclusion, see the greater percentages of errors for these problems in Table 2. The process of reasoning depends on models, and so language areas cease to be active as participants are inferring the answer for the logic problems. The models are maintained and manipulated by activity in inferior parietal and right frontal areas. In searching for counterexamples, reasoners try to construct a model that meets two independent goals: on the one hand, the model satisfies the premises; on the other hand, it refutes the conclusion. As the relational complexity of this process grows it depends increasingly on the right frontal pole.

Our results make clear that logical reasoning and mathematical thinking do rely in part on distinct neural substrates, and so high-level cognition does not depend solely on a

unitary global system. There may be regions common to both kinds of reasoning, but the finding of areas more specialized for logic only in the right frontal lobe, and for math only in the left frontal lobe, makes it clear the substrates for these kinds of reasoning differ. Logical reasoning goes beyond linguistic processing to the manipulation of non-linguistic representations.

4. Experimental procedures

The research was carried out in accordance with guidelines of the Princeton University Institutional Review Panel for Human Participants of the University Research Board, and the participants were screened for magnet compatibility and signed consent forms. They were shown examples of the problems before they entered the scanner in to familiarize them with the tasks. The logic problems were adapted from an earlier behavioral study in which participants were observed constructing with pencil and paper counterexamples on the hard logic problems. The math problems used prestatements and premises identical in form to those for the logic problems, so that the only differences between logic and math problems occurred at presentation of the conclusion. Each of the 16 participants in the fMRI study carried out 10 sets of trials in counterbalanced orders, and each set included one problem of each of the four sorts (easy logic, hard logic, easy math, and hard math problem) randomly ordered. On each trial, the participants saw a blank screen for 3 s, a fixation word ("READY") for 2 s, and then a statement (the "prestatement") setting up the problem for 3 s, at which time it was joined on screen by the three premises which together remained visible for 11 s. There was a blank screen for 1 s, and then the screen containing the conclusion to be evaluated, or mathematical formula to be checked, for 30 s. As soon as this screen appeared, the participants could begin to solve the problem. When they had decided whether or not the conclusion was valid (for the logical problems) or true (for the mathematical problems), they responded 'yes' or 'no' by pressing one of two buttons. A 14-second intertrial interval occurred before the

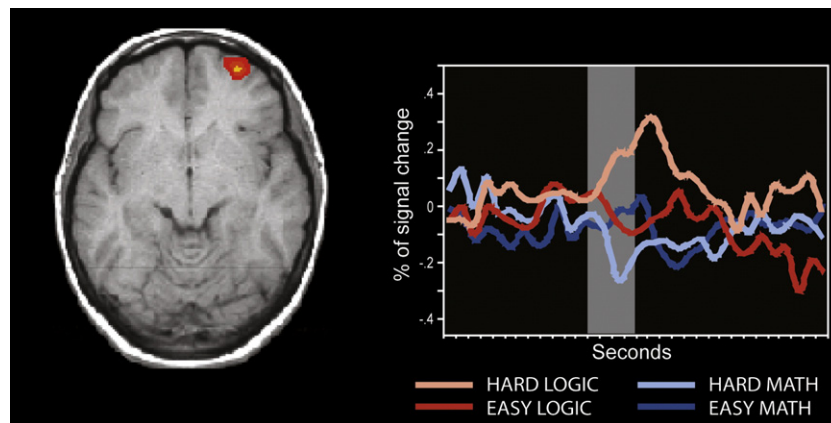


Fig. 5 – The interaction between the type of problem and level of difficulty in right frontal pole (BA 10). A planned comparison revealed that during the 8-second window, the hard logic problems activated this region more than the easy logic problems did. There was no difference between the hard and easy mathematical problems, and only the hard logic problems showed elevation above baseline.

next trial in order to permit the hemodynamic response to return to baseline level. The sequence of events in a trial is shown in Fig. 1. Each trial immediately followed the previous trial except between sets of four problems, when the participants rested for several seconds.

4.1. fMRI methodology

Thirty-two images were acquired during each trial (1.5-T GE Signa whole-body scanner, standard head coil). Functional images were acquired in 20 axial slices parallel to the AC–PC line (one-shot spiral pulse sequence; TR: 2000 ms; TE: 45 ms; flip angle: 80°; FOV: 240 mm; 3.75 mm isotropic voxels). Before the statistical analysis, the images for all participants were coregistered using a 12-parameter automatic algorithm. They were also smoothed using an 8 mm FWHM 3D Gaussian filter. Four participants were removed from one analysis due to motion artifact; this was determined using the AIR program (Woods et al., 1998).

4.2. fMRI analysis

To discover differences in the neural activity evoked by logical and mathematical problems, a voxel-wise analysis of variance (of problem type X difficulty) was performed on the four images in an 8-second interval starting 4 s after the presentation of the question (the shaded region in Fig. 1). This window was selected to compensate for hemodynamic lag and it was based on the solution times for easy problems, so that for both easy and hard problems, the participants would be calculating the solution during the entire window. This procedure ensured that any significant results reflected solely the differences in mental processes underlying the solution of the four sorts of problem and were not contaminated by differences in solution time for the easy and hard problems. The same analyses of variance were also carried out on the results for the entire solution period (30 s), on the results for the period between the presentation of the problem and the mean response time of the four sorts of problem, and on the results for the period between the presentation of the problem and each participant's response on each trial. All three of these analyses were carried out separately on all responses and on only the correct responses. In each case, the results were almost identical to those that we report for the 8-second window.

Significant regions of interest (ROIs) were revealed by thresholding statistical maps of voxel-wise *F*-ratios for significance. Only groups of six or more contiguous significantly active voxels are reported; this constraint corrects the results for multiple statistical comparisons across voxels. The cluster size threshold was selected using Monte Carlo simulations to achieve acceptable family-wise error rates ($p < .01$) given the spatial correlations in the functional data along with varying choices of voxel-wise significance thresholds. ROIs are clusters of voxels that each exhibited a significant difference in activation during solution of logic and math problems. All reported activations are voxel clusters found by voxel-wise thresholding which also meet the contiguity requirement. A planned comparison determined the directionality of differences (either greater activation during logic or during math

calculation) by thresholding maps of *t*-values (two-tailed) for these ROIs. Main effects for math vs. logic depicted in Fig. 2 were significant at a threshold of $p < .0001$. The interaction depicted in Fig. 5 was less strong but still significant, $p < .005$; and the planned comparison was significant at $p < .025$.

To determine whether ROIs of significant activation during the logic problems were active longer for the hard logic problems than for the easy ones, a *t*-test analysis was performed on those ROIs (using a mask) over the full 30-second response period, and significant voxels were thresholded ($p < .005$). The rationale of this analysis is that neural sites active longer in the hard problems than the easy ones must be those involved in the computation of the deduction. This analysis could reveal whether the total activation of the hard problems across the 30-second solution period was significantly greater than for the easy problems. Such a finding could indicate that the sites significantly more active for the hard problems were active for a longer time, and thus corresponded to the actual computation of the solution.

We attempted an analysis to determine areas of activation common to both math and logic problem solution, subtracting for each problem type activity for the easy problems from that for the hard problems, to find the intersection between these. The intersection was not computed since no significant differences were observed for the easy and hard math problems.

Acknowledgments

We thank Avital Polsky for the valuable help in preparing the manuscript. We thank Markus Knauff for the help and advice. The research was supported in part by a Young Investigator Award to the first author from National Association for Research on Schizophrenia and Depression, and in part by a National Science Foundation Grant (0076287) to the fourth author to study strategies in reasoning.

REFERENCES

- Adolphs, R., Tranel, D., Bechara, A., Damasio, H., Damasio, A.R., 1996. Neuropsychological approaches to reasoning and decision-making. In: Damasio, A.R. (Ed.), *Neurobiology of Decision-Making*. Springer-Verlag, Berlin, pp. 157–178.
- Baddeley, A., 1996. The fractionation of working memory. *Proc. Natl. Acad. Sci. U. S. A.* 93 (24), 13468–13472.
- Baddeley, A., 2000. The episodic buffer: a new component of working memory? *Trends Cogn. Sci.* 4 (11), 417–423.
- Berman, R.A., Colby, C.L., Genovese, C.R., Voyvodic, J.T., Luna, B., Thulborn, K.R., Sweeney, J.A., 1999. Cortical networks subserving pursuit and saccadic eye movements in humans: an fMRI study. *Hum. Brain Map.* 8 (4), 209–225.
- Braine, M.D.S., O'Brien, D.P., 1998. *Mental Logic*. Lawrence Erlbaum Associates, Mahwah, NJ.
- Braver, T.S., Cohen, J.D., Nystrom, L.E., Jonides, J., Smith, E.E., Noll, D.C., 1997. A parametric study of prefrontal cortex involvement in human working memory. *Neuroimage* 5 (1), 49–62.
- Brunetti, M., Della Penna, S., Ferretti, A., Del Gratta, C., Gianflone, F., Belardinelli, P., Caulo, M., Pizzella, V., Olivetti Belardinelli, M., Romani, G.L., 2007. A frontoparietal network

- for spatial attention reorienting in the auditory domain: a human fMRI/MEG study of functional and temporal dynamics. *Cereb. Cortex* 18 (5), 1139–1147.
- Buschman, T.J., Miller, E.K., 2007. Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* 315 (5820), 1860–1862.
- Canessa, N., Gorini, A., Cappa, S.F., Piattelli-Palmarini, M., Danna, M., Fazio, F., Perani, D., 2005. The effect of social content on deductive reasoning: an fMRI study. *Hum. Brain Mapp.* 26 (1), 30–43.
- Caplan, J.B., Luks, T.L., Simpson, G.V., Glaholt, M., McIntosh, A.R., 2006. Parallel networks operating across attentional deployment and motion processing: a multi-seed partial least squares fMRI study. *Neuroimage* 29 (4), 1192–1202.
- Cohen, J.D., Perlstein, W.M., Braver, T.S., Nystrom, L.E., Noll, D.C., Jonides, J., et al., 1997. Temporal dynamics of brain activation during a working memory task. *Nature* 386 (6625), 604–608.
- Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., et al., 1998. A common network of functional areas for attention and eye movements. *Neuron* 21 (4), 761–773.
- Dehaene, S., Spelke, E., Pinel, P., Stanescu, R., Tsivkin, S., 1999. Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science* 284 (5416), 970–974.
- Dehaene, S., Piazza, M., Pinel, P., Chen, L., 2003. Three parietal circuits for number processing. *Cogn. Neuropsychology* 20, 487–506.
- D'Esposito, M., Aguirre, G.K., Zarahn, E., Ballard, D., Shin, R.K., Lease, J., 1998. Functional MRI studies of spatial and nonspatial working memory. *Brain Res. Cogn. Brain Res.* 7 (1), 1–13.
- Dove, A., Pollmann, S., Schubert, T., Wiggins, C.J., von Cramon, D.Y., 2000. Prefrontal cortex activation in task switching: an event-related fMRI study. *Brain Res. Cogn. Brain Res.* 9 (1), 103–109.
- Duncan, J., Owen, A.M., 2000. Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci.* 23 (10), 475–483.
- Fangmeier, T., Knauff, M., Ruff, C.C., Sloutsky, V., 2006. FMRI evidence for a three-stage model of deductive reasoning. *J. Cogn. Neurosci.* 18 (3), 320–334.
- Fehr, T., Code, C., Herrmann, M., 2007. Common brain regions underlying different arithmetic operations as revealed by conjunct fMRI-BOLD activation. *Brain Res.* 1172, 93–102.
- Flechsig, P., 1901. Developmental (myelogenetic) localisation of the cerebral cortex in the human subject. *Lancet* 2, 1027–1029.
- Fuster, J.M., 2006. The cognit: a network model of cortical representation. *Int. J. Psychophysiol.* 60 (2), 125–132.
- Gazzaley, A., Rissman, J., Desposito, M., 2004. Functional connectivity during working memory maintenance. *Cogn. Affect. Behav. Neurosci.* 4 (4), 580–599.
- Gazzaniga, M.S., 1985. *The Social Brain*. Basic Books, New York.
- Gazzaniga, M.S., Smylie, C.S., 1984. Dissociation of language and cognition. *Brain* 107, 145–153.
- Gerstmann, J.F., 1924. Eine umschriebene Störung der Orientierung am eigenen Körper. *Wien. Klin. Wschr.* 37, 580–599.
- Goel, V., 2007. Anatomy of deductive reasoning. *Trends Cogn. Sci.* 11 (10), 435–441.
- Goel, V., Dolan, R.J., 2000. Anatomical segregation of component processes in an inductive inference task. *J. Cogn. Neurosci.* 12 (1), 110–119.
- Goel, V., Dolan, R.J., 2003a. Explaining modulation of reasoning by belief. *Cognition* 87 (1), B11–22.
- Goel, V., Dolan, R.J., 2003b. Reciprocal neural response within lateral and ventral medial prefrontal cortex during hot and cold reasoning. *Neuroimage* 20 (4), 2314–2321.
- Goel, V., Dolan, R.J., 2004. Differential involvement of left prefrontal cortex in inductive and deductive reasoning. *Cognition* 93 (3), B109–B121.
- Goel, V., Gold, B., Kapur, S., Houle, S., 1997. The seats of reason? An imaging study of deductive and inductive reasoning. *Neuroreport* 8 (5), 1305–1310.
- Goel, V., Gold, B., Kapur, S., Houle, S., 1998. Neuroanatomical correlates of human reasoning. *J. Cogn. Neurosci.* 10 (3), 293–302.
- Goel, V., Buchel, C., Frith, C., Dolan, R.J., 2000. Dissociation of mechanisms underlying syllogistic reasoning. *Neuroimage* 12 (5), 504–514.
- 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* 10, 2245–2250.
- Grabner, R.H., Ansari, D., Reishofer, G., Stern, E., Ebner, F., Neuper, C., 2007. Individual differences in mathematical competence predict parietal brain activation during mental calculation. *Neuroimage* 38 (2), 346–356.
- Gruber, O., Indefrey, P., Steinmetz, H., Kleinschmidt, A., 2001. Dissociating neural correlates of cognitive components in mental calculation. *Cereb. Cortex* 11 (4), 350–359.
- Habeck, C., Rakitin, B.C., Moeller, J., Scarmeas, N., Zarahn, E., Brown, T., et al., 2005. An event-related fMRI study of the neural networks underlying the encoding, maintenance, and retrieval phase in a delayed-match-to-sample task. *Brain Res. Cogn. Brain Res.* 23 (2–3), 207–220.
- Halford, G.S., Wilson, W.H., Phillips, S., 1998. Processing capacity defined by relational complexity: implications for comparative, developmental, and cognitive psychology. *Behav. Brain Sci.* 21 (6), 803–831 discussion 831–864.
- Henson, R.N., Burgess, N., Frith, C.D., 2000. Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study. *Neuropsychologia* 38 (4), 426–440.
- Holyoak, K.J., Thagard, P., 1995. *Mental Leaps: Analogy in Creative Thought*. MIT Press, Cambridge.
- Husain, M., Nachev, P., 2007. Space and the parietal cortex. *Trends Cogn. Sci.* 11 (1), 30–36.
- Inui, T., Otsu, Y., Tanaka, S., Okada, T., Nishizawa, S., Konishi, J., 1998. A functional MRI analysis of comprehension processes of Japanese sentences. *Neuroreport* 9 (14), 3325–3328.
- Jacobs, B., Schall, M., Prather, M., Kapler, E., Driscoll, L., Baca, S., et al., 2001. Regional dendritic and spine variation in human cerebral cortex: a quantitative Golgi study. *Cereb. Cortex* 11 (6), 558–571.
- Jancke, L., Kleinschmidt, A., Mirzazade, S., Shah, N.J., Freund, H.J., 2001. The role of the inferior parietal cortex in linking the tactile perception and manual construction of object shapes. *Cereb. Cortex* 11 (2), 114–121.
- Johnson-Laird, P.N., 1995. Models in deductive thinking. In: Gazzaniga, M.S. (Ed.), *The Cognitive Neurosciences*. MIT Press, Cambridge, MA.
- Johnson-Laird, P.N., Byrne, R.M., 1991. *Deduction*. L. Erlbaum Associates, Hillsdale.
- Johnson-Laird, P.N., Legrenzi, P., Girotto, P., Legrenzi, M.S., 2000. Illusions in reasoning about consistency. *Science* 288, 531–532.
- Knauff, M., Johnson-Laird, P.N., 2002. Visual imagery can impede reasoning. *Mem. Cognit.* 30 (3), 363–371.
- Knauff, M., Fangmeier, T., Ruff, C.C., Johnson-Laird, P.N., 2003. Reasoning, models, and images: behavioral measures and cortical activity. *J. Cognitive Neurosci.* 15 (4), 559–573.
- Kosslyn, S.M., 1994. *Image and Brain*. MIT Press, Cambridge, MA.
- Kosslyn, S.M., Ganis, G., Thompson, W.L., 2001. Neural foundations of imagery. *Nat. Rev. Neurosci.* 2 (9), 635–642.
- Kroger, J., Holyoak, K.J., 2004. Varieties of sameness: the impact of relational complexity on perceptual comparisons. *Cogn. Sci.* 28 (3), 335–358.
- Kroger, J.K., Sabb, F.W., Fales, C.L., Bookheimer, S.Y., Cohen, M.S., Holyoak, K.J., 2002. Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: a parametric study of relational complexity. *Cereb. Cortex* 12 (5), 477–485.

- Krueger, F., Fischer, R., Heinecke, A., Hagendorf, H., 2007. An fMRI investigation into the neural mechanisms of spatial attentional selection in a location-based negative priming task. *Brain Res.* 1174, 110–119.
- Lee, K.M., 2000. Cortical areas differentially involved in multiplication and subtraction: a functional magnetic resonance imaging study and correlation with a case of selective acalculia. *Ann. Neurol.* 48 (4), 657–661.
- Mayer, E., Martory, M.D., Pegna, A.J., Landis, T., Delavelle, J., Annoni, J.M., 1999. A pure case of Gerstmann syndrome with a subangular lesion. *Brain* 122 (Pt 6), 1107–1120.
- Mazoyer, B.M., Dehaene, S., Tzourio, N., Frak, V., Murayama, N., Cohen, L., et al., 1993. The cortical representation of speech. *Cogn. Neuroscience* 5 (4), 467–479.
- Melrose, R.J., Poulin, R.M., Stern, C.E., 2007. An fMRI investigation of the role of the basal ganglia in reasoning. *Brain Res.* 1142, 146–158.
- Menon, V., Rivera, S.M., White, C.D., Eliez, S., Glover, G.H., Reiss, A.L., 2000. Functional optimization of arithmetic processing in perfect performers. *Brain Res. Cogn. Brain Res.* 9 (3), 343–345.
- Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* 24, 167–202.
- Monti, M.M., Osherson, D.N., Martinez, M.J., Parsons, L.M., 2007. Functional neuroanatomy of deductive inference: a language-independent distributed network. *Neuroimage* 37 (3), 1005–1016.
- Neth, H., Johnson-Laird, P.N., 1999. The Search for Counterexamples in Human Reasoning. Paper presented at the 21st Annual Conference of the Cognitive Science Society, Vancouver.
- Ni, W., Constable, R.T., Mencl, W.E., Pugh, K.R., Fulbright, R.K., Shaywitz, S.E., et al., 2000. An event-related neuroimaging study distinguishing form and content in sentence processing. *J. Cogn. Neurosci.* 12 (1), 120–133.
- Noveck, I.A., Goel, V., Smith, K.W., 2004. The neural basis of conditional reasoning with arbitrary content. *Cortex* 40 (4–5), 613–622.
- Olesen, P.J., Nagy, Z., Westerberg, H., Klingberg, T., 2003. Combined analysis of DTI and fMRI data reveals a joint maturation of white and grey matter in a fronto-parietal network. *Brain Res. Cogn. Brain Res.* 18 (1), 48–57.
- Olesen, P.J., Macoveanu, J., Tegner, J., Klingberg, T., 2007. Brain activity related to working memory and distraction in children and adults. *Cereb. Cortex* 17 (5), 1047–1054.
- Osherson, D., Perani, D., Cappa, S., Schnur, T., Grassi, F., Fazio, F., 1998. Distinct brain loci in deductive versus probabilistic reasoning. *Neuropsychologia* 36 (4), 369–376.
- Parsons, L.M., Osherson, D., 2001. New evidence for distinct right and left brain systems for deductive versus probabilistic reasoning. *Cereb. Cortex* 11 (10), 954–965.
- Paulesu, E., Frith, C.D., Frackowiak, R.S., 1993. The neural correlates of the verbal component of working memory. *Nature* 362 (6418), 342–345.
- Peterson, S., Fox, P., Posner, M.I., Mintun, M.A., Mintun, R., 1989. Positron emission tomographic studies of the processing of single words. *J. Cogn. Neurosci.* 1 (2), 153–170.
- Petrides, M., Alivisatos, B., Evans, A.C., Meyer, E., 1993. Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. *Proc. Natl. Acad. Sci. U. S. A.* 90 (3), 873–877.
- Price, C.J., 2000. The anatomy of language: contributions from functional neuroimaging. *J. Anat.* 197 (Pt 3), 335–359.
- Price, C.J., Wise, R.J., Warburton, E.A., Moore, C.J., Howard, D., Patterson, K., et al., 1996. Hearing and saying. The functional neuro-anatomy of auditory word processing. *Brain* 119 (Pt 3), 919–931.
- Rips, L.J., 1994. *The Psychology of Proof*. MIT Press, Cambridge, MA.
- Robin, N., Holyoak, K.J., 1995. Relational complexity and the functions of prefrontal cortex. In: Gazzaniga, M.S. (Ed.), *The Cognitive Neurosciences*. MIT Press, Cambridge, MA, pp. 987–997.
- Rushworth, M.F., Krams, M., Passingham, R.E., 2001. The attentional role of the left parietal cortex: the distinct lateralization and localization of motor attention in the human brain. *J. Cogn. Neurosci.* 13 (5), 698–710.
- Rypma, B., Prabhakaran, V., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 1999. Load-dependent roles of frontal brain regions in the maintenance of working memory. *Neuroimage* 9 (2), 216–226.
- Sabb, F.W., Bilder, R.M., Chou, M., Bookheimer, S.Y., 2007. Working memory effects on semantic processing: priming differences in pars orbitalis. *Neuroimage* 37 (1), 311–322.
- Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., Van Hoesen, G.W., 2001. Prefrontal cortex in humans and apes: a comparative study of area 10. *Am. J. Phys. Anthropol.* 114 (3), 224–241.
- Shallice, T., 1988. *From Neuropsychology to Mental Structure*. Cambridge University Press, Cambridge.
- Shaw, P., Greenstein, D., Lerch, J., Clasen, L., Lenroot, R., Gogtay, N., et al., 2006. Intellectual ability and cortical development in children and adolescents. *Nature* 440 (7084), 676–679.
- Simon, O., Mangin, J.F., Cohen, L., Le Bihan, D., Dehaene, S., 2002. Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron* 33 (3), 475–487.
- Simon, O., Kherif, F., Flandin, G., Poline, J.B., Riviere, D., Mangin, J.F., et al., 2004. Automated clustering and functional geometry of human parietofrontal networks for language, space, and number. *Neuroimage* 23 (3), 1192–1202.
- Slotnick, S.D., Moo, L.R., 2006. Prefrontal cortex hemispheric specialization for categorical and coordinate visual spatial memory. *Neuropsychologia* 44 (9), 1560–1568.
- Smith, E.E., Jonides, J., 1998. Neuroimaging analyses of human working memory. *Proc. Natl. Acad. Sci. U. S. A.* 95 (20), 12061–12068.
- Smith, E.E., Jonides, J., Koeppe, R.A., 1996. Dissociating verbal and spatial working memory using PET. *Cereb. Cortex* 6 (1), 11–20.
- Stromsworld, K., Alpert, N., Rausch, S., Caplan, D., 1996. Localization of sentence processing using positron emission tomography. *Brain Language* 52, 452–473.
- Swartz, B.E., Halgren, E., Fuster, J., Mandelkern, M., 1994. An 18FDG-PET study of cortical activation during a short-term visual memory task in humans. *Neuroreport* 5 (8), 925–928.
- Tanaka, S., Inui, T., Iwaki, S., Konishi, J., Nakai, T., 2001. Neural substrates involved in imitating finger configurations: an fMRI study. *Neuroreport* 12 (6), 1171–1174.
- Thompson-Schill, S.L., D'Esposito, M., Aguirre, G.K., Farah, M.J., 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc. Natl. Acad. Sci. U. S. A.* 94 (26), 14792–14797.
- Travis, K., Jacobs, B., 2003. Regional dendritic variation in neonatal human cortex: a quantitative Golgi analysis. *Behav. Neurosci.* 1, 8–16.
- Ungerleider, L.G., Haxby, J.V., 1994. 'What' and 'where' in the human brain. *Curr. Opin. Neurobiol.* 4 (2), 157–165.
- Vallar, G., 2007. Spatial neglect, Balint-Homes' and Gerstmann's syndrome, and other spatial disorders. *CNS Spectr.* 12 (7), 527–536.
- van Harskamp, N.J., Rudge, P., Cipolotti, L., 2005. Does the left inferior parietal lobule contribute to multiplication facts? *Cortex* 41 (6), 742–752.
- Varley, R., Siegal, M., 2000. Evidence for cognition without grammar from causal reasoning and 'theory of mind' in an agrammatic aphasic patient. *Curr. Biol.* 10, 723–726.
- Veltman, D.J., Rombouts, S.A., Dolan, R.J., 2003. Maintenance versus manipulation in verbal working memory revisited: an fMRI study. *Neuroimage* 18 (2), 247–256.
- Wager, T.D., Smith, E.E., 2003. Neuroimaging studies of working memory: a meta-analysis. *Cogn. Affect. Behav. Neurosci.* 3 (4), 255–274.

- Wager, T.D., Jonides, J., Smith, E.E., Nichols, T.E., 2005. Toward a taxonomy of attention shifting: individual differences in fMRI during multiple shift types. *Cogn. Affect. Behav. Neurosci.* 5 (2), 127–143.
- Waltz, J.A., Knowlton, B.J., Holyoak, K.J., Boone, K.B., Mishkin, F.S., de Menezes Santos, M., et al., 1999. A system for relational reasoning in human prefrontal cortex. *Psych. Science* 10, 119–125.
- Waltz, J.A., Knowlton, B.J., Holyoak, K.J., Boone, K.B., Back-Madruga, C., McPherson, S., et al., 2004. Relational integration and executive function in Alzheimer's disease. *Neuropsychology* 18 (2), 296–305.
- Wharton, C.M., Grafman, J., 1998. Deductive reasoning and the brain. *Trends Cogn. Sci.* 2, 54–59.
- Woods, R.P., Grafton, S.T., Holmes, C.J., Cherry, S.R., Mazziotta, J.C., 1998. Automated image registration: I General methods and intrasubject, intramodality validation. *Comput. Assist. Tomogr.* 22, 139–152.
- Yeh, Y.Y., Kuo, B.C., Liu, H.L., 2007. The neural correlates of attention orienting in visuospatial working memory for detecting feature and conjunction changes. *Brain Res.* 1130 (1), 146–157.