The dynamics of deductive reasoning: An fMRI investigation

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A R T I C L E   I N F O

A B S T R A C T

Although the basis for deductive reasoning has been a traditional focus of philosophical discussion, the neural correlates and mechanisms that underlie deductive reasoning have only recently become the focus of scientific investigation. In syllogistic deductive reasoning information presented in two related sequential premises leads to a subsequent conclusion. While previous imaging studies have identified frontal, parietal, temporal, and occipital complexes that are activated during these reasoning events, there are substantive differences among the findings with respect to the specific regions engaged in reasoning and the contribution of language areas. Further, little is known about the various stages of information processing during reasoning. Using event-related fMRI and an auditory and visual conjunction technique, we identified a long-range supramodal network active during reasoning processes including areas in the left frontal and parietal regions as well as the bilateral caudate nucleus. Time courses of activation for each of these regions suggest that reasoning processes emerge during the presentation of the second premise, and remain active until the validation of the conclusion. Thus, areas within the frontal and parietal regions are differentially engaged at different time points in the reasoning process consistent with coordinated intra-network interactions.

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1. Introduction

1.1. Psychological models of deductive reasoning

One of the most advanced intellectual abilities of humans is the capacity to reason. In deductive reasoning, the reasoning starts with a set of premises and generates a conclusion not explicitly stated on the initial premises. In the case of syllogisms, there are only two premises which contain a term in common and two terms that are distinct. For example, in the syllogism 'All lions are wild animals. All wild animals have fur. Therefore, all lions have fur.' the premises share the term 'wild animals', and the terms 'lions' and 'fur' are the distinct terms. The syllogistic inference is based on the relation between the two distinct terms that are linked through the common term.

Syllogistic reasoning has historically been the subject of active philosophic and psychological inquiry, and only recently have specific models of encoding and reasoning mechanisms been proposed (see for example Braine, 1978; Evans, 2006; Henle, 1962; Johnson-Laird & Byrne, 1991; Newell & Simon, 1972; Osherson, 1975; Rips, 1983; Sloman, 1996). However, few psychological theories make predictions of the neural substrate underlying syllogistic reasoning and the neural substrate for deductive reasoning remains relatively unexplored. The Mental Logic theory of reasoning (Braine, 1978; Henle, 1962; Rips, 1994) suggests that reasoning relies on a language-like structure and therefore should be supported by left-hemisphere language areas. On the other hand, the Mental Model theory of reasoning (Johnson-Laird & Byrne, 1991; Johnson-Laird, 1994) proposes that reasoning is rooted in mental sets of the situation presented by the premises, and those sets are spatial in nature. Accordingly, reasoning functions would be expected to be mediated in regions specialized for visualization such as right-hemisphere parieto-occipital areas involved in visuospatial processing.

Although most psychological theories divide deductive reasoning into three stages: premise encoding, premise integration, and conclusion validation (Braine & O'Brien, 1991; Chater & Oaksford, 1999; Cheng & Holyoak, 1985; Evans, Barston, & Pollard, 1983; Johnson-Laird & Byrne, 1991; Polk & Newell, 1995; Rips, 1983; Rader & Sloutsky, 2002; Sloman, 1996), it is not known if these sequential stages are carried out by different brain areas.

1.2. Functional localization of deductive reasoning

Imaging studies have been inconclusive with respect to the neural substrates that sustain deductive reasoning. Goel, Buchel,

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Frith, and Dolan (2000) have reported a dual-pathway system for categorical syllogisms that consists of a left frontal–temporal network mainly in memory and language-dependent areas and a visuospatial network involving right parietal areas. In addition, the left-hemisphere system would be recruited for familiar or belief-laden content of the arguments while the right-hemisphere system would be more engaged for belief-neutral content of the arguments. Studies using relational spatial reasoning also support this functional dissociation (Goel & Dolan, 2001; Goel, Makale, & Grafman, 2004). On the other hand, Osherson et al. (1998) observed a right-hemispheric network including language-homologue areas when categorical syllogistic arguments were checked for deductive validity. These results were replicated in a follow-up study conducted by Parsons and Osherson (2001) using conditional syllogisms. Studies by Knauff and colleagues have shown the involvement of a fronto-parietal–occipital network for the solution of linear syllogisms (three-term series problems) (Knauff, Mulack, Kassubek, Salih, & Greenlee, 2002) and conditional and relational arguments (Knauff, Fangmeier, Ruff, & Johnson-Laird, 2003) presented orally suggesting a role of visuospatial processes in reasoning. Houde et al. (2000) described a shift from posterior brain regions to left prefrontal cortex as subjects' performance in a conditional reasoning task improved after bias-inhibition training. Recently, Fangmeier, Knauff, Ruff, and Sloutsky, (2006) described the involvement of bilateral prefrontal, occipital and parietal areas for the solution of relational spatial syllogisms. Monti, Osherson, Martinez, and
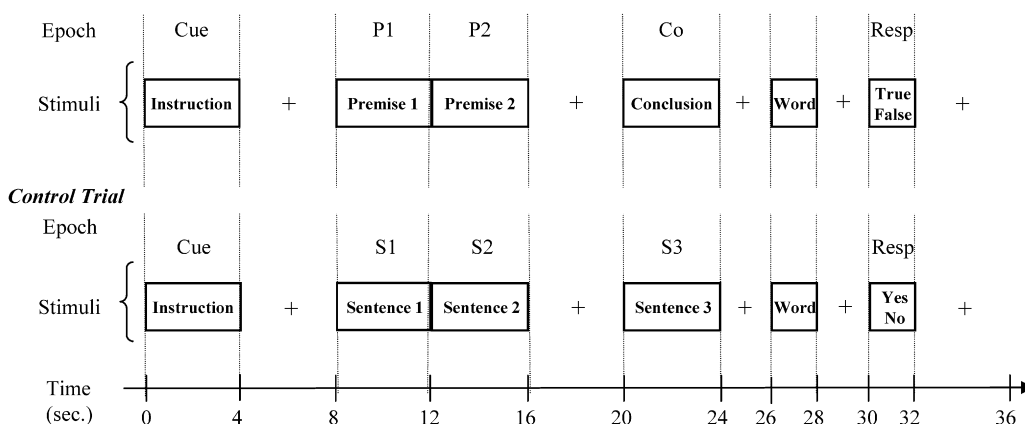
Parsons (2007) showed the involvement of a left prefrontal and parietal network for conditional reasoning and pointed out the lack of engagement of language areas during the task. In contrast, a later report by Reverberi et al. (2007) supports the view of Broca's (and left parietal) engagement in reasoning with conditional and disjunctive arguments. The diversity of results regarding the substrate engaged during reasoning tasks undoubtedly reflects both methodological and task variants in experimental approaches as well as the complexity of reasoning.

One of the possible factors responsible for the diversity of imaging results may be the use of different control conditions across different studies (Parsons & Osherson, 2001). Isolation of processes uniquely related to reasoning requires the exclusion of reasoning processes during the control task. For example, subjects prompted with two premises and asked to just 'rest' or perform a task other than reasoning might nonetheless engage automatic reasoning functions. Another factor that may introduce variance across imaging studies is the use of different stimulus modalities, i.e., visual and auditory. Although initial visual or auditory input can be separated from reasoning using an appropriate control task, and visual and auditory processes might converge at high-level reasoning areas, whereas intermediate processes of reasoning might be modality specific.

Finally, imaging studies of deductive reasoning have typically employed block designs precluding the separation of possible stages of reasoning as recently suggested (Fangmeier, Knauff, Ruff,

a. Experimental Design

Fig. 1. Stimulus presentation. (a) Experimental design. The layout of a single trial is shown for the reasoning and the control tasks. r indicates rest, P1 indicates premise 1 encoding, P2 indicates premise 2 encoding and premise integration, Co indicates validation of the conclusion, and Resp indicates response time. (b) Sample stimuli for the deduction and the control tasks.

& Sloutsky, 2006). Nonetheless, this study employed visuospatial reasoning and therefore may not be extended to deductive reasoning using language input. A newer study by Reverberi et al. (2007) aimed to separate conclusion generation from premise encoding and conclusion validation supports the involvement of a frontal–parietal network for reasoning. It is not clear if those results are specific to disjunctive and conditional arguments or can be generalized to other deductive reasoning tasks. Hence, it remains unresolved if language areas are necessary for sentence-based reasoning, or which brain regions are modality-independent, and to what extent those areas contribute to different stages of deductive reasoning.

1.3. Aims of the present study

Using functional magnetic resonance imaging (fMRI) and a mixed event-related design, we intended to isolate the specific areas involved in supramodal reasoning, and to differentiate their engagement during the different stages of deduction. In addition, we aimed to investigate the contribution of language regions to reasoning processes.

In the current study, the three sentences of the reasoning or the control task were presented sequentially (Fig. 1a). Problems with linguistic content were used because we wanted to investigate the involvement of language in a realistic scenario of everyday reasoning. A cue at the beginning of each trial indicated if it was a reasoning or control trial. Sentences were presented visually or aurally in order to dissociate brain regions related to high-level reasoning from those related to sensory processes and low-level reasoning. Cross-modal strategies have been previously employed to isolate substrates associated with high-level cross-modal cognitive systems (Buchel, Price, & Friston, 1998; Hirsch, Rodriguez-Moreno, & Kim, 2001; Schumacher et al., 1996).

The reasoning trials consisted of categorical syllogisms and subjects were instructed to generate a conclusion from the premises, read/listen to the conclusion provided by the experimenter, and indicate whether the provided conclusion was "True" or "False" with a motor response (Fig. 1b). The control task consisted of three unrelated sentences so no reasoning could be applied to them. It employed the same time series of three sequential sentences and maintained all structural characteristics of the reasoning task. However, to distinguish from the reasoning processes, the sentences were unrelated, that is, did not contain terms in common that would prompt reasoning processes. For example: "All bears are wild animals", "All green vegetables are healthy foods", and "Some countries are wealthy" have no terms in common. In addition, the control task was chosen to isolate language processing from the reasoning task. It required subjects to process sentences throughout the trial as reasoning tasks without the need of language manipulation presumably involved during premise integration in deduction.

To investigate the temporal dynamics of syllogistic reasoning we looked at the areas engaged during premise encoding, premise integration, and conclusion validation phases in comparison to the language-based control task. Thus, premise encoding would encompass the reading/listening of the premises. The integration of the premises in a unified representation would initiate the onset of reasoning and subsequent generation of the subject's conclusion. The final validation of the conclusion would include a comparison between the subjects' and the experimenter's conclusion.

The control task in this experiment was designed to keep the subjects engaged until the end of the trial as with the reasoning task. In addition, at the end of the trial the subject indicated if a target word (viewed briefly) was present or not in any of the sentences to ensure that the sentences were encoded, and that their content was maintained in working memory throughout the trial. The key difference between the reasoning and the control task was that the sentences could be integrated into a unique representation in the reasoning task but they could not be integrated in the control task. Therefore, the control task required the maintenance of the sentences in working memory as it was required in the reasoning task but lacking the components that could lead to syllogistic reasoning.

1.4. Predicted imaging results and their relevance

The fMRI activity associated with the underlying reasoning processes can be isolated by comparing the syllogistic reasoning with the control task at each stage of the trials. We expected to cancel out all linguistic activity associated to input (sentence encoding) and output (conclusion generation and validation) processing. The remaining activity in language areas, if any, will provide evidence for the involvement of linguistic processes in reasoning. In addition, we hypothesized that there would be a group of supramodal areas observed in common between visual and auditory reasoning that would represent the neural substrate that is more central for language-based deductive reasoning.

The use of a control task that matched the temporal dynamics of the reasoning task allowed us to predict the patterns of activity for each stage of the trials that would be obtained when the reasoning task was compared to the control task. We predicted that the neural process associated with only encoding, which happens during the encoding of the first premise of the syllogism, would be similar to the neural process associated with the encoding of the first sentence of the control task. Therefore, a subtraction strategy would result in an absence of activation during encoding of the first premise. Premise integration, including conclusion generation, was expected to occur during premise 2. Comparison with the second sentence of the control (assumed to encode without integration due to the absence of common terms) was expected to isolate activation associated to premise integration. Similarly, conclusion encoding and validation were expected to occur at the time that the experimenter's conclusion was given. The activity associated with the validation process would be isolated by subtraction of the activity associated with of the third sentence of the control task. The processes of premise encoding, integration and conclusion validation could be carried out by either the same set of brain regions or by recruitment of different brain regions as the function progresses. Differential involvement of brain regions across reasoning stages would support cognitive models of reasoning that separate deduction into premise encoding, premise integration and conclusion validation.

Finally, we addressed the notion that reasoning is carried out by supramodal reasoning network with the idea that there might be modality specific-regions for reasoning. We looked at patterns of activity for each reasoning modality separately to identify the involvement of modality specific regions during the stages of reasoning. We hypothesized that there would be modality-specific areas engaged during reasoning in comparison with the control task that represent intermediate processes of reasoning, and would contribute to a supramodal network of reasoning to carry out the deduction.

2. Methods

2.1. Subjects

Twelve healthy volunteers, (3 males and 9 females, mean age 26.6 ± 5.6 years) without history of neurological disorders or chronic disease, were recruited according to institutional informed consent procedures. The study was approved by Institution's ethics committee and performed in accordance with the Declaration of Helsinki. One subject was unable to finish the task and was excluded from the analysis. All subjects were right-handed (laterality quotient 89.58 ± 12.07) as assessed by the Edinburgh handedness inventory (Oldfield, 1971). Structural MRI revealed no

brain abnormalities in any of the subjects. Reaction times were acquired subsequent to the scanning sessions in a similar cohort of subjects (3 females and 5 males, mean age of 28.8 ± 6.8 years).

2.2. Reasoning and control tasks

The time course of reasoning and control trials are shown in Fig. 1a and correspondent trial examples are given in Fig. 1b. Each trial started with the presentation of an instructional cue (Cue) that indicated whether the trial was a reasoning trial or a control trial. The cue for the reasoning trials was 'Is the conclusion true or false?' The cue for the control trials was 'Is the word present or absent?' In both reasoning and control tasks subjects were instructed to give their answer when the response was prompted at the end of the trial alternating right and left response hands between runs. Subjects were instructed to respond as soon as the response choices were presented.

The reasoning trials consisted of categorical syllogisms, which contained a quantifier term ('all', 'some', 'none') in each of the premises as well as the conclusion. Half of the syllogisms were valid and half invalid (Fig. 1b). The three parts of the syllogisms were presented sequentially: premise 1 (P1), premise 2 (P2) and conclusion (Co). Subjects were instructed to attend to the premises and to draw a conclusion at their own pace after the presentation of the second premise. Subjects then were instructed to attend to the experimenter's conclusion, decide if it was true or false, and indicate their response when they were prompted with the 'True' or 'False' choices after a delay of 6 s (Resp) alternating right and left response hands between runs. Since subjects did not have previous training in logic, the response choices used for the reasoning trials were 'True' and 'False' instead of the logical terms 'Valid' and 'Invalid'.

The control trials consisted of a word recognition task that was presented in the same format as the syllogisms. The task consisted of a set of three unrelated sentences presented sequentially in the same way as the syllogisms, followed by a target word. The three parts of the control task were presented sequentially: sentence 1 (S1), sentence 2 (S2) and sentence 3 (S3). The subjects were instructed to determine whether the target word had been included in any of the three previous sentences, half the time the word was present and half of the time it was absent. The target word was given at the end of the trials to assure that the subjects had attended to all three sentences (to equate the control and reasoning trials, the syllogisms were also followed by a word, but in that case the word was ignored, since it was not necessary to solve the syllogisms). Subjects indicated their response choice ('Yes' or 'No') at the end of the trial during the response (Resp) epoch.

2.3. Stimulus presentation

Trials were presented in a mixed event-related design with 8 separate runs. Each run consisted of 9 task or control trials randomly intermixed, each trial lasting 36 s (Fig. 1a). During the reasoning trials, the cue, the first premise, the second premise, and the conclusion were presented sequentially for 4 s each. Similarly, during the control trials, the cue, the first sentence, the second sentence, and the third sentence were presented sequentially for 4 s each. The target word and the response choices were presented for 2 s each. To separate cognitive events associated to each sentence in the trial, we added resting state delays indicated by a "+" in Fig. 1a. The first delay (4 s) between the cue and the first premise was employed to separate the preparation for the trial from the activation related to encoding the first premise. The second delay (4 s) between the presentations of the second premise and the conclusion separated premise integration from conclusion validation. The third delay (6 s) was positioned between the conclusion and the response in order to separate the effects of conclusion validation from the motor response. Similar delays were used during the control trials. Additionally, an inter-trial delay (4 s) was placed between the response and the cue of the following trial to allow time for any reasoning processes to diminish before the start of the next trial. A fixed inter-trial delay, as opposed to a jittered delay, was employed since the duration of the trials was much longer than the minimum 15 s that provides the most efficient estimation of the BOLD responses to discrete events (Burock, Buckner, Woldorff, Rosen, & Dale, 1998; Dale, 1999). In addition, the randomization of reasoning and control trials provided a natural jitter to the reasoning components of the experiment given by involvement of different processes on each type of trial.

Four of the runs employed visual stimuli and four of the runs employed auditory stimuli. The visual stimuli were back projected onto a screen located in front of the subject as viewed through the slanted mirror located above the head coil. The auditory stimuli were presented through headphones designed to reduce background scanner noise (Resonance Technology, Inc.). The two stimulus modalities were interleaved and the order varied across subjects. Before the scanning session, each subject received a training session of two runs, one on each stimulus modality, to familiarize them with the tasks and assure a clear understanding of the instructions.

2.4. Imaging

A 1.5-T General Electric (LX) magnetic resonance scanner with a standard head coil was used to obtain T2*-weighted images with a gradient echo pulse sequence (echo time, 60 ms; flip angle, 60°; repetition time, 4000 ms). This sequence was

selected to taking into account constraints for run length, sample size and scanner capacity for file size. Twenty-one contiguous slices of brain were obtained parallel to the AC/PC line, a standard reference line that intersected the superior edge of the anterior commissure and the inferior edge of the posterior commissure. The 21 slices covered the entire cortex of the cerebrum for all subjects. The field of view was 190 mm and each slice was imaged in a 128 by 128 voxel matrix. The in-plane resolution was approximately 1.5 mm by 1.5 mm and slice thickness was 4.5 mm. Conventional high-resolution (T1-weighted) images were also acquired along sagittal planes and at the same axial plane locations as the T2*-weighted images during each imaging session. Each run consisted of 106 images, each consisting of one brain volume of the whole brain, and required an imaging time of 7 min and 4 s. Each session consisted of eight runs.

2.5. fMRI data analysis

The initial four images of each run were not used for the analysis in order to assure that all acquisitions were at a common level of magnetic susceptibility. Data processing and analysis were performed with SPM99 software (Wellcome Department of Imaging Neuroscience, Institute of Neurology, University College London, London, UK). Preprocessing steps included slice-timing correction for interleaved acquisitions, motion correction using a sync interpolation algorithm, and normalization to MNI's EPI template of 152 brains using a 12-parameter affine transformation followed by nonlinear deformations. The spatial matrix was interpolated from 1.5 mm × 1.5 mm × 4.5 mm to an isotropic voxel size of 2 mm^3. Finally, smoothing was performed with a 6 mm full-width-half-maximum Gaussian kernel. In the time-course model specification, the blood-oxygenated level-dependent (BOLD) response was represented by a boxcar function for each part of the trial. The ideal box-car was convolved with the canonical hemodynamic response function (hrf). Global mean scaling for each run was performed. A high-pass filter of twice the length of the longest interval between two similar trials was used to remove low frequency confounds. The time-courses were also low-pass filtered with an hrf shape to replace the unknown temporal autocorrelations.

A within-subject (first-level) analysis was performed using SPM99 (Friston et al., 1995) using a one-sample *t*-test ($p = 0.001$, minimum cluster size = 20 voxels). For each run five contrasts were performed: (reasoning−control) for the cue (Cue), the first premise (P1), the second premise (P2), the conclusion (Co) and the response (Resp) epochs. The contrast images of single subjects were entered into a random-effects (second-level) across-subjects analysis as implemented by SPM99 ($p = 0.005$, minimum cluster size = 40 voxels) to allow for inferences at the population level. In addition, activations common across both presentation modalities (visual and auditory) for the reasoning tasks against their controls were extracted by applying a mask image to the corresponding group analysis of the visual reasoning task against its control. The mask image was created based in the activation observed for the group analysis of the auditory reasoning against its control. The extent of activation observed for most regions for the visual conditions was smaller than that of the auditory. Therefore, a minimum cluster size of 15 voxels was required in the masking procedure in order to ensure the detection of activations in the visual condition. Anatomical location and Brodmann areas were assigned to each cluster using the WFU_Pickatlas software (Maldjin, Laurienti, Burdette, and Kraft, 2003).

Time-course analysis was performed using the VOI tool of SPM. The filtered, non-adjusted signal for each cluster was obtained for every subjects for all runs. This signal, representing the average of the signals in the cluster, was then normalized to account for different baseline levels. The average signal was pooled by trial type (deduction or control) and across subjects using Microsoft Excel. Task and control trials were averaged across runs of the same input modality.

The volume ratio (V) of auditory and visual conditions for each cluster was used to compare the extent of activation in the two sensory modalities. For each cluster, it was obtained by dividing the number of voxels in the auditory modality by the number of voxels in the visual modality as obtained from the SPM analysis. So, a $V = 1$ will indicate the same extent of activation, while $V > 1$ will indicate greater extent of activation for the auditory modality than the visual modality and $V < 1$ will indicate smaller extent of activation for the auditory modality than the visual modality.

3. Results

3.1. Behavioral measures

Subjects' accuracy within each modality was similar in the reasoning and control tasks as indicated by the percent of correct responses: 96.5% (±3.8) for the visual control task, 96.5% (±4.5) for the visual reasoning task, 92.9% (±4.4) for the auditory control task, and 92.9% (±5.6) for the auditory reasoning task (Table 1). A two-factor ANOVA failed to confirm a difference between the control and reasoning task performances ($F(1, 40) = 0$, $p = 1$). However, the difference between auditory and visual modalities was shown to be significant ($F(1, 40) = 6.12$, $p = 0.018$) with a 3.6% better

Table 1
Subject information and percent correct responses.

Subject	Visual performance		Auditory performance	
	Control	Deduction	Control	Deduction
A	94	100	94	94
B	94	100	94	83
C	100	100	89	100
D	100	89	89	89
E	94	100	89	94
F	94	94	100	100
G	100	94	100	89
H	100	100	94	89
I	89	89	89	94
J	100	94	94	100
K	94	100	89	89
Mean	96.46	96.46	92.93	92.93
S.D.	3.75	4.49	4.37	5.61

performance in the visual modality, although no interaction between task and modality was observed ($F(1, 40) = 0$, $p = 1$).

3.2. fMRI results

3.2.1. Brain regions in common for visual and auditory modalities for each reasoning stage in comparison to the control task

For both visual and auditory modalities together, activity associated with the reasoning task in contrast to the control task engages a small network of regions (Table 2). This network includes the left supplementary motor area (SMA, BA 6/8), dorsolateral prefrontal cortex (DLPFC, BA 9), middle frontal (BA 10), ventrolateral prefrontal cortex (VLPFC, BA 47), right SMA (BA 8), the posterior parietal cortex (PPC, BA 7 and BA 40) and inferior parietal lobules (BA 9 and 40), and bilateral caudate nuclei. As predicted, the use of a cross-modal design excluded the sensory input processing areas in the occipital and temporal cortices from the supramodal reasoning network. In addition, traditional language areas were not part of the core network for the solution of syllogisms even though the stimuli were English sentences.

Although we looked at the overlapping regions active during visual and auditory reasoning, most of the clusters for each individual modality did not completely overlap. Indeed, the extent of activation was more extensive for the auditory condition, as reflected by the ratio of the number of activated voxels between the auditory and the visual tasks in Table 2 (V, in columns 3 and 4).

As expected, the supramodal reasoning network is observed from the onset of the second premise (P2) through the conclusion (Co). Activity during the instructions (Cue), the first premise (P1), and the response (Resp) was not different from the control and therefore are not shown in the table. Thus this analysis shows no activations at those time points. In addition, the data shows the engagement of different brain patterns during the different stages of reasoning. During P2 (column 3), corresponding to premise integration and conclusion generation, left superior and middle frontal cortices (Brodmann Area (BA) 6 and 8), left inferior parietal lobule (BA 40), superior parietal lobule (BA 7), and angular gyrus (BA 39) are more engaged during the reasoning than during the control task. During the Co (column 4), corresponding to conclusion validation, the left superior frontal gyrus (BA 6), the left middle frontal gyrus (BA 9 and 10), the right medial frontal gyrus (BA 8), the left inferior frontal gyrus (BA 47), bilateral inferior parietal lobules (BA 40) extending to supramarginal gyrus on the left side and bilateral caudate nuclei are each more active during the reasoning task than during the control task.

3.2.2. Separate time courses for reasoning and control tasks for visual and auditory modalities

Although the t-maps and their corresponding summary tables are informative regarding the regions active during different parts of the process, they provide only a partial picture of the underlying BOLD signal. A more informative look is provided by the actual time courses of the responses. The analysis of the time course associated separately with each task (reasoning and control) reveals additional information regarding the contributions of each region to the reasoning process. The inset time panels in Figs. 2 and 3 show the size of the effect at each time point of the reasoning process for the activated clusters listed in Table 2. Fig. 2 shows representative clusters active during the second premise (P2) associated with premise

Table 2
Brain regions for visual and auditory modalities conjoined (reasoning > control).

Anatomic Location	BA	Premise 2[a]					Conclusion[b]				
		x	y	z	Z	V	x	y	z	Z	V
Frontal											
L middle	8/6	−40	14	44	3.6	3.0					
L superior (SMA)	8/6	−2	33	48	3.8	1.6					
L superior (SMA)	6	−2	18	54	3.5	4.4	−6	34	52	3.7	3.7
L middle (DLPFC)	9						−36	21	36	3.5	16
L middle	10						−44	42	−5	2.9	4.9
R medial (SMA)	8						6	26	45	3.3	2.0
L inferior (VLPFC)	47						−44	17	−6	3.2	2.8
Parietal											
L inferior	40	−50	−46	48	3.7	1.1					
L superior/angular/inferior	7/39/40	−44	−58	49	3.3	2.6					
L supramarginal/inferior	40						−57	−47	24	4.0	1.1
R inferior	40						53	−50	47	4.1	1.9
Basal ganglia											
L caudate							−8	1	11	4.2	3.0
R caudate/thalamus							12	4	11	3.7	2.6

Activity was observed during the second premise and the conclusion presentation epochs only.
x, y, z indicate Talairach coordinates for the peak of activation in the cluster, BA indicates the Brodmann's Area, Z indicates the maximum z-score for the cluster and V indicates the volume ratio between auditory and visual conditions.
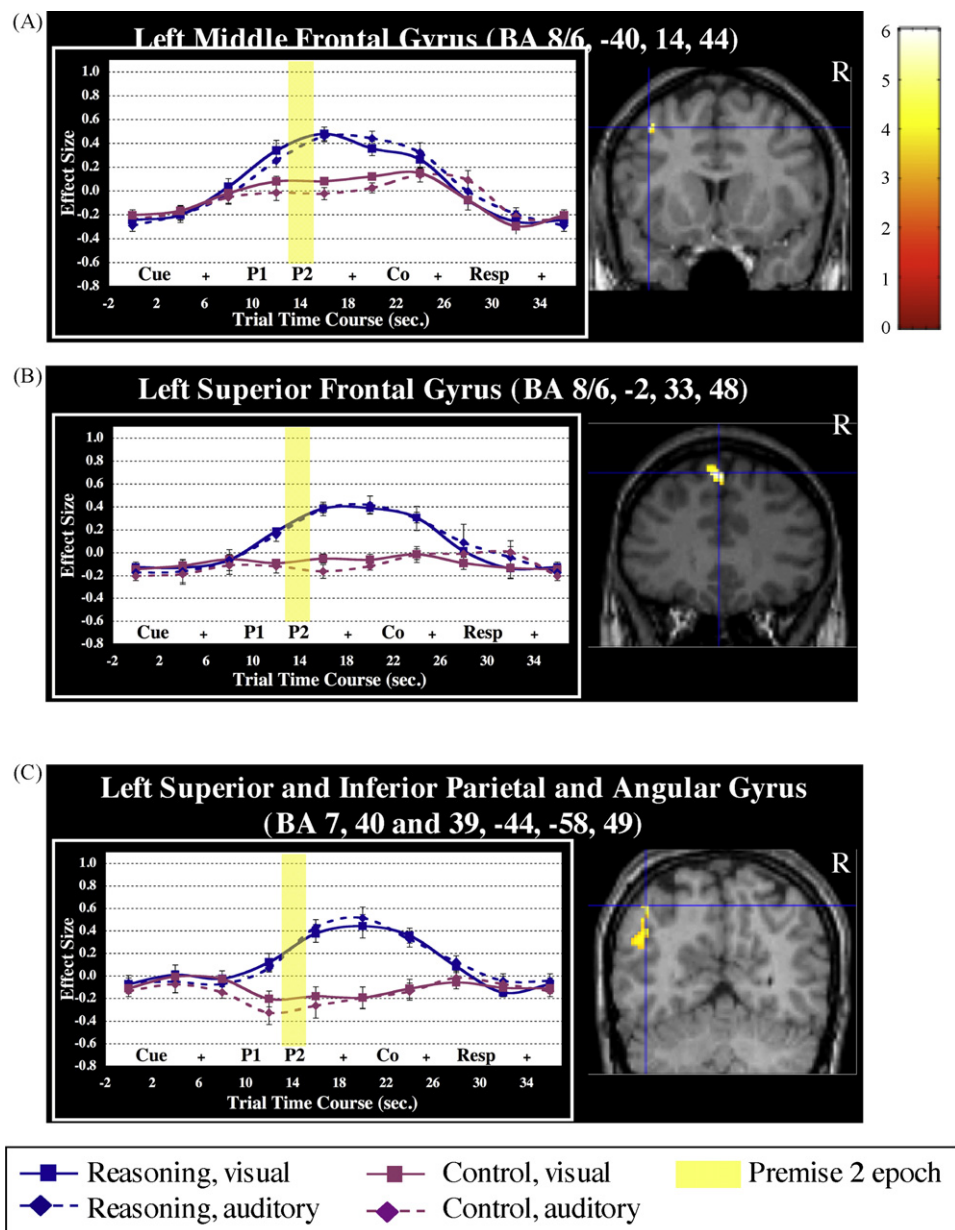[a] See Fig. 2(A)–(C).
[b] See Fig. 3(A)–(D).

Fig. 2. Supramodal reasoning activations during the second premise. Brain regions differentially active during reasoning across subjects for both visual and auditory modality for each epoch type corresponding to clusters present during the second premise according to Table 2. Activation t-maps are shown overlaid in coronal high-resolution anatomical images of a single subject. The graphs show the time course of activation for the whole cluster. Blue lines indicates the reasoning task, pink lines indicate the control task. Solid line with squares indicates the stimuli presented visually, dotted line with diamonds indicates the stimuli presented aurally. Error bars correspond to the standard errors at each time point. The yellow bar indicates the time second sentence is expected to peak considering a 6 s hemodynamic delay. The expected times for all parts of the trial are also indicated (cue, r: rest, P1: premise1, P2: premise 2, Co: conclusion, and Resp: response).

integration and conclusion generation (indicated by a vertical yellow bar) and Fig. 3 shows representative clusters active during the conclusion (Co) associated with conclusion validation (also indicated by a vertical yellow bar). The clusters of activity are shown in coronal slices for each of the active brain regions with their corresponding BA and Talairach coordinates. The time courses for the reasoning (blue) and the control (pink) tasks represent the activity of all the voxels and across all the subjects for the corresponding cluster. The activity is plotted taking into account an expected hemodynamic delay of 6 s.

A central observation from Figs. 2 and 3 is that activity uniquely associated with the reasoning task is significantly elevated from premise 2 encoding throughout the conclusion validation stage in most regions. This pattern was the same for both auditory and visual

modalities. These findings complement the previous results shown in Table 2. The sustained peak of activity is presumably composed of several neural processes that underlie premise 2 encoding (namely, encoding of the premise, premise integration and generation of the subjects' conclusion) and validation of the experimenter's conclusion. These processes are expected to have different temporal courses, with encoding of premise 2 at the beginning of the peak, premise integration and conclusion generation occur towards the middle of the peak, and conclusion validation at the end. An exception to this general pattern of activity is observed in the right inferior parietal (Fig. 3C). This region shows a small decrease of activity during P2 and a later increase during the Co epoch. This finding indicates that the right PPC is uniquely related to conclusion validation.
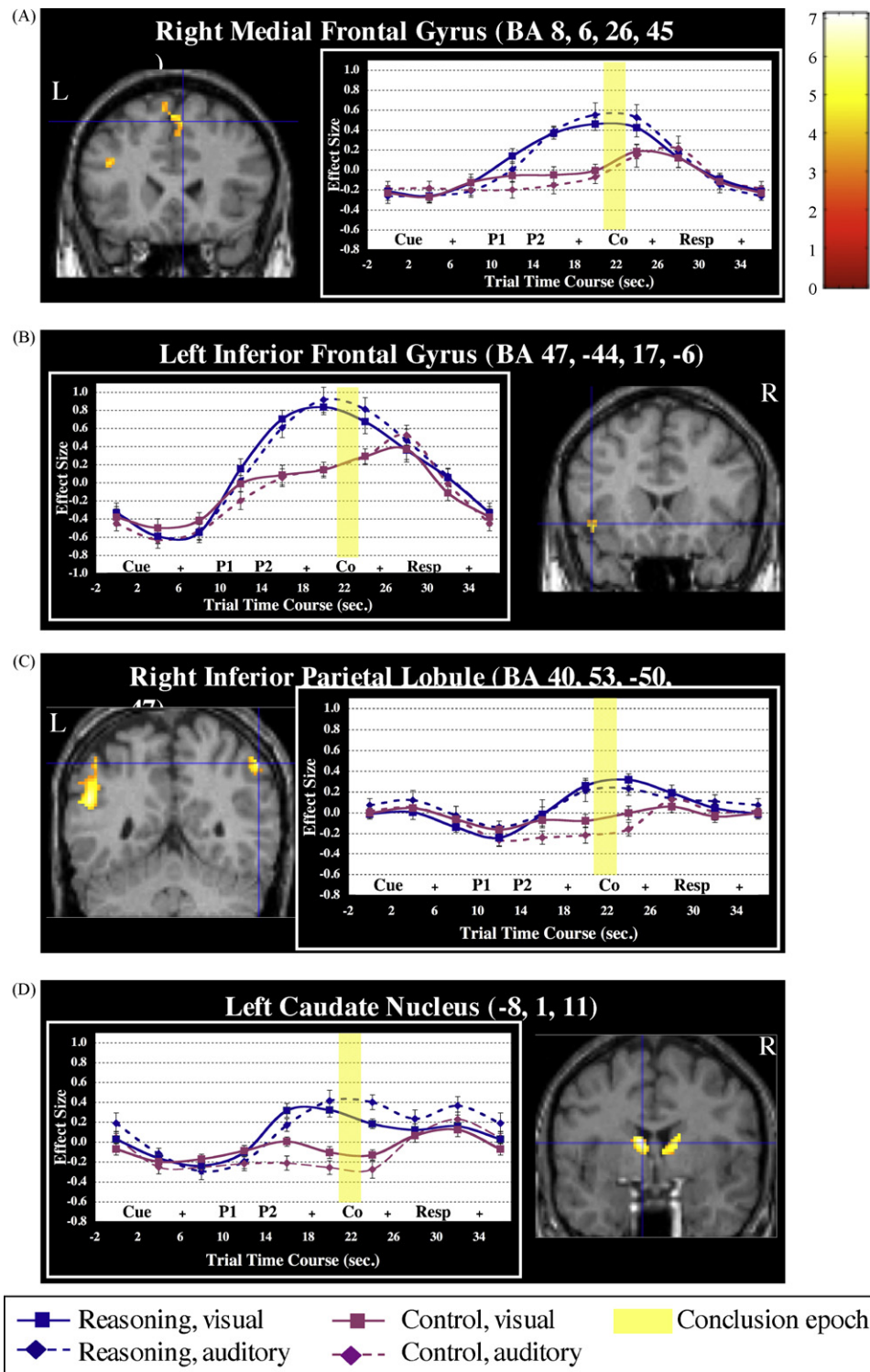
Fig. 3. Supramodal reasoning activations during the conclusion. Brain regions differentially active during reasoning across subjects for both visual and auditory modality for each epoch type corresponding to clusters present during the conclusion according to Table 2. Activation t-maps are shown overlaid in coronal high-resolution anatomical images of a single subject. The graphs show the time course of activation for the whole cluster. Blue lines indicates the reasoning task, pink lines indicate the control task. Solid line with squares indicates the stimuli presented visually, dotted line with diamonds indicates the stimuli presented aurally. Error bars correspond to the standard errors at each time point. Error bars correspond to the standard errors at each time point. The yellow bar indicates the time the conclusion is expected to peak considering a 6 s hemodynamic delay. The expected times for all parts of the trial are also indicated (cue, r: rest, P1: premise1 encoding, P2: premise 2 encoding and premise integration, Co: conclusion validation, and Resp: response).

When the activity associated with the control task is compared with that of the reasoning task, it informs about the cognitive processes involved in reasoning. Activation of the reasoning task, but not the control task, suggests the presence of processes unique to reasoning. We assume that regions that are engaged in the reasoning task during premises and/or conclusion epochs, but not during the control task, constitute the 'core regions' for reasoning, and they included the left superior frontal gyrus (BA 6/8, Fig. 2B), right medial frontal gyrus (BA 8) and the bilateral parietal lobule (BA 39/40/7, Figs. 2C and 3C). Contrary to the previous scenario, activation of the control task that parallels that of the reasoning task suggests the presence of similar underlying processes in the deduction and the control task. Those regions where activity is observed for reasoning and control tasks during premise and conclusion epochs can be assumed to carry out processes that are presumably necessary but not unique for reasoning and we refer to them as 'support regions'. Support regions included the left superior frontal gyrus (BA 6), the left middle frontal gyrus (BA 8/6; and BA9 and 10), and the left inferior frontal gyrus (BA 47). Finally, some of the core regions, including the right medial frontal gyrus (Fig. 3A), the bilateral inferior parietal lobule (BA 40) and left supramarginal gyrus (BA 40); and some of the support regions, including middle frontal gyrus (Fig. 2A), superior frontal gyrus, and middle frontal gyrus show a small peak of activation of the control task associated with the response time pointing towards their involvement on response preparation.

Although deduction time-courses are generally very similar across brain regions associated with reasoning, the caudate nucleus constitutes the exception (Fig. 3D). These time courses are different with respect to the other areas because they show two distinct peaks of activation during the reasoning task suggesting involvement in two separate underlying processes. These processes can involve an initial process uniquely related to reasoning and a later one related to preparing or executing a response. Therefore the caudate may be part of the core reasoning areas as well as one of the support regions for related processes, depending on the time of engagement. The time courses for the caudate are also different with respect to the sensory modalities. In the case of visual stimuli presentations activity has a larger peak at P2 and a smaller one at Resp epoch. In the auditory modality the peaks have similar height and occur between P2 and Co and at Resp epoch. The initial peak of BOLD signal that happens earlier for the visual than for the auditory modality may partially reflect a difference in encoding times as observed in a separate behavioral study (Rodriguez-Moreno, 2005). In fact, for the reasoning task visual sentences take an average of 2.25 ± 0.68 s to be processed while auditory sentences take 3.73 ± 0.3 s. A similar delay is observed for the control task in which second sentence encoding takes on the average 1.91 ± 0.67 s for the visual modality and 3.6 ± 0.35 s for the auditory modality. However, for the control tasks the difference in reaction time between modalities is not coupled to an earlier peak of the BOLD signal for the visual modality. This discrepancy between reaction times and BOLD signal time courses for reasoning and control tasks suggests that the delay in auditory activity during reasoning reflects more than the differences in encoding time.

In conclusion, the analysis of the time courses expands the results shown in Table 2 suggesting that areas observed during P2 (yellow bar in Fig. 2) are related to premise encoding or premise integration, areas observed during Co (yellow bar in Fig. 3) are related to conclusion validation. Furthermore, some areas show sustained activity from P2 to Co suggesting both their early involvement in premise integration and conclusion generation and also later involvement in validation of the conclusion. In addition, these results support the view that reasoning is composed of several underlying processes that are carried out by a group of brain regions that are differentially involved during the stages of deduction. Core

regions (left superior frontal, BA 6/8; right medial frontal gyrus, BA 8; bilateral parietal lobule, BA 39/40/7; and bilateral caudate) presumably carry out processes unique to reasoning, while support regions (left superior and middle frontal gyrus, BA 6/8/9/10; inferior frontal gyrus, BA 47; and caudate) presumably carry out other processes like maintenance, rehearsal, etc., that are shared with the control task. Although the underlying processes might be more continuous than originally expected, we have shown that they can be separated using an appropriately designed control task and by analyzing their time courses.

3.2.3. Brain regions for each individual modality (reasoning > control)

For each individual sensory modality, activity associated with the reasoning task in contrast to the control task engages a large network of regions. These networks encompass the previously observed crossmodal regions (mentioned in Section 3.2.1 and shown in bold in Supplementary Table 1 and 2) and modality specific regions not observed in the previous analysis. This finding supports the view that reasoning is carried out by a supramodal network of brain regions that work together with modality-specific networks.

These modality-specific networks show no clear involvement of language regions during reasoning. Visual deductive reasoning shows no activity in inferior frontal gyrus (BA 44/45) or the superior temporal gyrus (BA 22), while auditory deductive reasoning shows no activity in the left superior temporal cortex suggesting lack of involvement of Wernicke's Area in reasoning. Although the left inferior frontal cortex was observed during the conclusion epoch for auditory reasoning, this cluster was positioned on BA 47/45 rather than BA 44 corresponding to Broca's Area. Overall these results indicate the lack of involvement of language processes in deductive reasoning even for modality-specific reasoning.

Activity associated with visual syllogisms (Supplementary Table 1) during the Cue is observed in the bilateral anterior cingulate and the right caudate. P1 engages the left insula, right parahippocampal gyrus, bilateral anterior cingulate gyrus extending to medial and middle frontal cortices. P2 recruits additional clusters of the left dorsolateral prefrontal cortex accompanied by activation of bilateral caudate. Co activates the same regions as the auditory condition, with no areas uniquely engaged for the visual modality. Resp recruits the right superior/medial frontal and left inferior parietal and supramarginal gyrus and left posterior cingulated gyrus.

Activity associated with auditory syllogisms (Supplementary Table 2) during the Cue is observed in the right anterior cingulate, right precuneus, bilateral superior frontal gyrus extending to middle and medial frontal cortices, and right pre- and post-central gyrus. P1 engages right superior temporal cortex, right parahippocampal gyrus, left anterior cingulate gyrus, right inferior frontal gyrus including a portion of insula, bilateral middle frontal cortex, left inferior parietal and precuneus and left caudate. P2 activates the left middle temporal gyrus, the right middle frontal and the left precentral gyrus. Co activates additional areas of the frontal cortex, including left inferior frontal, bilateral middle frontal and left superior frontal, as well as bilateral precuneus. Resp recruits the right middle and superior temporal gyrus as well as the left inferior parietal lobule.

4. Discussion

The fundamental findings of this study are that (1) syllogistic reasoning activates a unique set of areas (left frontal-parietal-caudate system) that can be dissociated from traditional language areas even when the stimulus employed is linguistic; (2) broadly

overlapping regions of activation are engaged in both visual and auditory modalities suggesting that deductive reasoning engages a supramodal neural system; (3) areas engaged during deductive reasoning carry out processes unique to reasoning (core regions) and processes shared with the control task (support regions); and (4) activations of distinct brain regions are associated with different temporal stages of reasoning.

4.1. Separating reasoning processes from language processes

The design of this study identified a frontal–parietal–caudate supramodal reasoning network that is dissociable from the inferior frontal gyrus (BA 44, Broca's Area) and the superior temporal gyrus (BA 22, Wernicke's Area) that have been reported in previous reasoning studies (Goel, Gold, Kapur, & Houle, 1997; Goel et al., 2000, 2004; Knauff et al., 2003; Reverberi et al., 2007) and are considered classical language areas. This was true for both visual and auditory modalities. The involvement of language areas is observed for both modalities when they are not contrasted with the control task. Although current models of language (Hickok & Poeppel, 2004; Ullman, 2004) also relate the frontal areas to the memory components of language, they focus on Broca's area in the inferior frontal gyrus (BA 44 and 45), an area that we do not observe in our study. In addition, we observed increased activity in the inferior frontal gyrus (BA 47) relative to the control task and the resting baseline during reasoning epochs. Although this region could constitute a language component of reasoning, alternative explanations are possible. For example, BA 47 has been reported to have a role in cognitive control of semantic memory retrieval (Badre & Wagner, 2007) besides the roles attributed by language studies in semantics (i.e., Hagoort, 2005; McDermott, Petersen, Watson, & Ojemann, 2003) or in strategic inferences (Chow, Kaup, Raabe, & Greenlee, 2008). Thus, while we observed that some language areas were activated in the overall reasoning task, our results are most consistent with the conclusion that reasoning engages internal representations that do not include traditional language areas. This finding suggests that the internal representation over which reasoning is done is not necessarily a linguistic one. The use of a control task that closely matched the language components of the reasoning tasks presumably separated the contribution of language processes that may be necessary but not central to the reasoning functions associated with the syllogism task. A similar separation between reasoning and language systems has been recently reported by Monti et al. (2007) using conditional arguments. On the other hand, the presence of language areas in previous studies likely was due to the use of different control conditions to which the reasoning task was compared. For example, some studies used control tasks where subjects had to disengage from the control task after the second premise and continue in a resting state for the remainder of the trial (Goel & Dolan, 2001; Goel et al., 2004). Thus, control tasks using either syllogisms or two related premises may have engaged processes involved in integration of information required during reasoning. The presence of traditional language areas was also observed in reasoning studies without an explicit control experimental condition (Knauff et al., 2002; Knauff & Johnson-Laird, 2002, 2003). Reverberi et al. (2007) found significant activations in the left frontal gyrus (BA 44) while subjects generated conclusions to simple reasoning tasks. The difference in results with our study cannot be explained based on control conditions, since they also used sentences that could not be integrated as a control condition. The disparity of results may indicate real differences in the neural networks recruited for syllogistic and propositional reasoning. Based on our results we suggest that although language may be required for syllogistic reasoning, it can be partitioned from the core of the reasoning process.

4.2. A supramodal network for deductive reasoning

The network isolated for deductive reasoning was independent of the input modality, and included regions of the PFC (middle frontal (BA 8/6, BA 9 and 10), left superior frontal (BA 6, 8), medial frontal (BA 8) and inferior frontal (BA 47)), regions of the PPC (superior and inferior parietal regions (BA 40, 39, 7)), as well as bilateral caudate nucleus. The identification of a supramodal network for deductive reasoning was possible by excluding the effects of control task with similar input and output requirements to the reasoning task but which explicitly did not elicit reasoning processes. Reasoning can be seen as a process that requires the same initial input processing as the control, but differs from it with respect to the relationships of the terms contained in the premises. Further, presumably there are also specific brain regions engaged for each separate modality and the conjunction across modalities allowed the isolation of cross modal regions that are most representative of the reasoning process.

The conjoined used of our control task and the cross modal approach revealed that the solution of categorical syllogisms (reasoning) is associated with activity originating during the encoding of the second premise and continuing through the conclusion. We did not observe supramodal areas associated with the cue, the first premise, or the response indicating that at the early and late stages of reasoning most of the activity was either related to processing of stimuli similar to the control task or modality-dependent.

Although some of the regions observed in this frontal-parietal-caudate network have been reported in previous neuroimaging deductive reasoning studies (Goel et al., 2000; Goel & Dolan, 2001, 2004; Houde et al., 2000; Knauff et al., 2002; Osherson et al., 1998), those studies also reported areas that were related to modality specific processes.

4.3. Core and support regions for deductive reasoning

The present results indicate that reasoning is a highly complex cognitive process that relies on frontal and parietal areas previously linked to working memory, attention and language in numerous studies (for a review see Cabeza & Nyberg, 2000). The similar timecourses, but with different amplitudes, for both for the reasoning and the control tasks in some of the regions of our supramodal network suggests that some underlying neuronal processes might be shared between tasks, but the load of these processes might be different as shown in Figs. 2A and 3B. Areas that share those common processes during the premises and/or conclusion epochs for the reasoning and control tasks are referred to as 'support regions', and include left superior and middle frontal gyrus, BA 6/9/10; and inferior frontal gyrus, BA 47. Regions that are engaged only during the reasoning task are referred to as 'core regions' for reasoning and consist of left superior frontal, BA 6/8; right medial frontal gyrus (BA 8) and bilateral parietal lobule, BA 39/40/7. These results are in agreement with recent results on conditional reasoning (Monti et al., 2007) that used task load instead of a control task to parse out reasoning from other cognitive processes. Our paradigm also shows the engagement of basal ganglia that has not been observed in previous work probably due to similar engagement of caudate in low and high load reasoning conditions. Caudate responds as both, a core and a support region, as it is engaged only by the reasoning task during premise integration/conclusion generation and by both tasks at the response time.

4.4. Brain regions associated with stages of deductive reasoning

Deductive reasoning includes premise encoding, premise integration and conclusion-validation stages. The later two stages are
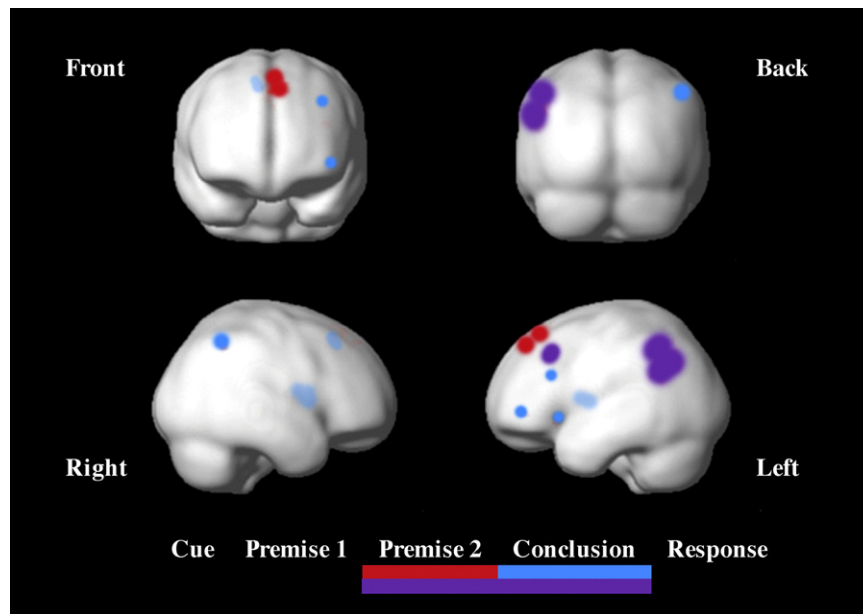
Fig. 4. Summary of supramodal reasoning network. The scheme shows the shift of activation from superior frontal and parietal regions during the second premise (red) to a more spread network in the left frontal lobe, bilateral parietal and caudate nucleus during the conclusion (blue). Some subset of these regions show sustained activity through sentence two and conclusion (purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

carried out by a supramodal network and span over the P2 and Co epochs. We observe a progression of areas recruited during the reasoning process as shown in Table 2. Middle frontal cortex (BA 8/6) is primarily engaged during the P2 (Fig. 4, areas in red), and left superior frontal cortex (BA 6, 8) and left parietal regions (BA 40, 39, 7) exhibit a sustained pattern of activation during P2 and the Co (Fig. 4, areas in purple). Additional regions are recruited during Co, including left frontal regions of the middle (BA 9 and 10), medial (BA 8) and inferior (BA 47) frontal gyri, as well as bilateral caudate nucleus (Fig. 4, areas in blue).

Premise encoding involves the transformation of the visual/auditory input stimuli into a neural representation. The absence of enhanced activation during premise 1 in this study indicates that premise 1 encoding is similar to the control task of simple sentence encoding. The longer reaction time to encode the second premise than to encode the first premise suggests that encoding of the second premise is concurrent with other processes, presumably integration of premises. Similarly, the greater BOLD signal in most areas during premise 2 encoding than during sentence 2 (control) encoding indicates the engagement of these regions in premise integration rather than simply input processing. An earlier increase of activity on the left middle frontal cortex (BA 6/8, Fig. 2A) and the parallel activation of the control task suggest that this area is mainly engaged in premise encoding.

The integration of the premise initiates the reasoning-specific process and leads to the generation of the subject's conclusion. A separate behavioral study (Rodriguez-Moreno, 2005) showed that premise integration and conclusion generation happened before the experimenter's conclusion was given. For the visual reasoning trials, conclusion generation took on average 4.65 ± 0.87 s so approximately 3.4 s passed before conclusion validation. For the auditory reasoning trials, conclusion generation took on average 5.48 ± 0.73 s, therefore 2.52 s passed before conclusion validation. The behavioral results confirm that we achieved a separation of premise integration/conclusion generation from conclusion validation.

All regions observed in the present study, with the exception of caudate nucleus and right inferior parietal lobule, presented

activity sustained from P2 to Co associated to the deduction task suggesting their involvement in premise integration and conclusion validation. However, the lack of activity during the control task in clusters in the core regions, in contrast with some pattern of activity during the control task in clusters in the support regions, suggest that the role of these areas in premise integration and conclusion validation is different.

The observed activation of clusters in the frontal cortex only in deduction tasks (core regions in the left superior frontal, BA 6; and right medial frontal, BA 8) is presumably involved in integrating terms of the premises and possibly in the initial manipulation of the terms, while the clusters in the frontal cortex that also show sustained activation during the control task (support regions in the left middle frontal, BA 6/8, Fig. 2A; and middle frontal, BA 9 and BA 10; left superior frontal gyrus BA 6; and inferior frontal gyrus BA 47, Fig. 3B) might be more related to maintaining and updating information that are also required during the control task. Middle and superior frontal gyri have been associated with executive functions of working memory (Wager & Smith, 2003). Those areas are involved in updating of information in working memory, that is required by control and reasoning tasks, and are also sensitive to the temporal order of the items that appears to be necessary for subjects to solve the syllogisms. Similarly, the middle frontal cortex (BA10)'s function in working memory (Lee, Robbins, Graham, & Owen, 2002), storage of object, verbal and spatial information in working memory (Wager & Smith, 2003), and generation/maintenance of an attentional set (Buckner, 2003) could play a role in both reasoning and control tasks. However, other studies suggest that BA 10 could play a role in processes required only by a reasoning task such as manipulation and continuous information updating (Wager & Smith, 2003), in relational integration (Christoff et al., 2001) and premise integration (Fangmeier et al., 2006). In addition, the control task peaks towards the end of the trial in several core and support clusters (the right medial frontal gyrus (BA8), the left middle frontal gyrus (Fig. 2A) and left superior frontal gyrus) suggesting a common involvement of these areas in reasoning and control tasks for response preparation.

Clusters in the parietal lobule did not have any control-related activity and constitute core regions that span over the left superior (LPS) and bilateral inferior (LPI) parietal lobules and angular gyrus (Fig. 2C). A similar parietal activation was observed for reasoning versus baseline tasks bilaterally (left BA 40, $x = −42$, $y = −51$, $z = 48$; and right BA 40, $x = 36$, $y = −48$, $z = 48$) in the work of Goel and Dolan (2001). The left inferior parietal lobules and left supramarginal region show an increase of activation during the control task at the response time suggesting common processes for the deduction and control tasks at the response epoch. Parietal lobule has been associated with a wide variety of functions including working memory, attention, visuospatial manipulations, and language. It has been proposed that angular gyrus and the temporo-parietal junction are jointly involved in mapping between phonetic and motor representations of language processing (Hickok & Poeppel, 2004; Ullman, 2004) and phonological storage of verbal working memory (Baddeley, 2003; Wager & Smith, 2003). Superior parietal regions are thought to be involved in attention-related systems. For example, top-down (goal-directed) visual attention has been shown to activate dorsal parietal cortex along the intraparietal sulcus (IPS) extending dorsomedially to LPS and the frontal eye fields (Corbetta & Shulman, 2002). In addition, the maintenance of an attentional set associated with working memory may be mediated by sustained activity of parietal and lateral prefrontal cortices. Superior parietal regions are also related to attentional selection during language processing. However, the control task was designed to control for attentional and language processes and therefore should show similar activity. An alternative interpretation is that parietal cortices observed during syllogistic reasoning reflect the involvement of executive processes (i.e., manipulation) that interact dynamically with attentional processes, as suggested by Gruber and Goschke (2004). Parietal regions spanning the IPS and the LPS have been also associated with keeping track of temporal order of items in working memory (Wager & Smith, 2003) that is presumably a requirement unique to the reasoning process. Therefore, our study supports the view that clusters in LPS, dorsal LPI, angular gyrus and supramarginal gyrus carry out executive processes unique to the reasoning task.

Lateral prefrontal cortex (dorsal BA 46, medial BA 44 and BA 45, and ventral BA 47 of the inferior frontal gyrus) has been proposed to be involved in the encoding and retrieval of verbal information and declarative knowledge (Buckner & Wheeler, 2001; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner et al., 1998), and in verbal storage (Wager & Smith, 2003). The presence of inferior frontal cortex (BA 47) among the supramodal reasoning areas could be interpreted as a higher demand of verbal encoding and/or storage during the reasoning compared to the control task. However, given that the syllogisms and the control sentences were matched in length the requirement for verbal encoding and storage should be similar. An alternative interpretation could be that the left inferior frontal gyrus (BA 47) is associated with the manipulation of the sentences elements necessary to solve the syllogisms according to the role of BA 47 ($x = 46$, $y = 22$, $z = −11$) in the manipulation of complex sentence structures in working memory (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004). The time-course of the signal in BA 47 (Fig. 3E) suggests that a combination of both processes may occur. Indeed, both reasoning and control tasks recruit this area. Reasoning-related activity tends to peak at the time the conclusion is generated. However, the control task elicits a further increase of activation around the response time when the target word is retrieved from the sentences. Findings from our study suggest that inferior frontal gyrus is part of a support network required but not essential for deductive reasoning.

Caudate nucleus in both hemispheres was the only brain region that shows two peaks of activation during the reasoning task (i.e.,

left caudate, Fig. 3D). The first peak occurred around P2 while the later peak correlates with Resp. The different shape of caudate time-courses suggests that its involvement in the deductive reasoning is of a different nature than the other brain regions. Furthermore, time-courses of activation of the control tasks show only a peak at the response epoch, presumably related to execution of the motor response. The role of caudate nucleus in cognition is a current subject of active investigation. Ullman proposes that basal ganglia, thalamus, and Broca's area are part of a procedural memory system that is required for grammar (Ullman, 2004). Accordingly, this system plays a role in selection and maintenance of working memory including representation of complex linguistic information and the rules applied to those representations. Although it is quite possible that reasoning requires increased use of working memory for maintenance and manipulation of information respect to the control task, the activity of caudate in our results is not accompanied by activation in Broca's area. On the other hand, activity in the basal ganglia has been observed in tasks that require sequencing, like the Raven's Progressive Matrices (Christoff et al., 2001), the Serial Reaction Time task (Schendan, Searl, Merose, & Stern, 2003), and semantic event sequencing task (Tinaz, Schendan, Schon, & Stern, 2006). Recent fMRI evidence suggests dissociation between the head and the body of the caudate with respect to its role in reasoning (Melrose, Poulin, & Stern, 2007). Accordingly, the head of the left caudate is more involved during the deduction and application of a sequence than during a simple matching task, while the bilateral body of the caudate is engaged during both tasks. A similar caudate activity is obtained in our study, although without the anatomical specificity proposed by those authors.

The final step of deductive reasoning consists of the validation of the conclusion and includes a comparison between the subjects' and the experimenter's conclusion. Activity uniquely associated with conclusion-validation is initiated when the experimenter's conclusion is presented. The activation of right parietal lobule (Fig. 3C) at the conclusion epoch suggests that this area is uniquely associated with the conclusion-validation task rather than premise integration and conclusion generation. Furthermore, the absence of activity for the control task in this area suggests the engagement of this region on processes that are unique to reasoning. Right parietal regions are known to play a role in spatial tasks. It is possible that the comparison of the conclusions requires a visuospatial approach that would engage this area. However, the parietal clusters reported here are more dorsal and lateral than previously reported peak coordinates for visuospatial tasks that engage intraparietal sulcus ($x = −28$, $y = −64$, $z = 48$) and the inferior parietal cortex ($x = −32$, $y = −48$, $z = 44$) (Jordan, Heinze, Lutz, Kanowski, & Jancke, 2001).

These data suggest that brain regions are differentially engaged at different time points of reasoning. In retrospect, a higher temporal resolution, either using shorter TR or jittered intervals between the premises and the conclusion, might enhance the differentiation between areas involved in each stage of reasoning. Nonetheless, due to the time difference between the beginning of the second premise and the validation of the conclusion, the temporal resolution used in the study was sufficient to isolate areas uniquely associated with conclusion validation. Our results are in agreement with those of Fangmeier et al. (2006), although some differences are also observed. Using similar contrasts, both studies failed to observe activity associated with initial premise encoding, while bilateral prefrontal cortex was associated with premise integration and conclusion-validation, and right parietal cortex was associated with conclusion validation. However, the coordinates for those areas vary between the studies, possibly due to differences in the control tasks and in the nature of the stimuli (spatial vs. linguistic). Only activation of the left middle frontal gyrus (BA 6) on the pre-

frontal cortex has the exact same peak coordinates ($x = -40$, $y = 14$, $z = 44$). Furthermore, similar results have been obtained by Monti et al. (2007) using a different reasoning and control tasks. We extend and confirm previous findings by identifying brain areas that are closely related to reasoning (core regions) versus those that are less related (support regions).

4.5. Modality-specific regions for deductive reasoning

While overlapping activation between modalities suggest a supramodal deductive reasoning network for deduction, distinction between the visual and auditory modalities was also observed and constitutes a novel finding. Specifically, our results show that auditory reasoning is more bilateral and frontal biased than is visual reasoning. Possible explanation for this finding may be related to the accuracy results suggesting that reasoning with auditorily presented stimuli may have been more difficult than with the visual stimuli. Likewise, it could also be related to the longer encoding time for the auditory condition observed in the reaction time results. Whatever the explanation for this modality specificity, these results suggest that reasoning requires modality-specific components that work together with supramodal reasoning regions to carry out the deduction.

Even when the functions of the observed active regions are considered in the context of current knowledge of brain functions, conclusive interpretations of the role of these regions in the reasoning tasks employed here are limited. The present study focused on the relation of these areas to postulated phases of deductive reasoning (premise encoding, premise integration, and conclusion validation) and on the dynamics of those areas. Further studies that manipulate the language, working memory and other cognitive processes are required to elucidate exact roles of those areas in reasoning. Additionally, the temporal resolution of fMRI is limited compared to EEG and MEG, and understanding of the reasoning dynamics would benefit by further studies using these high-temporal resolution techniques.

4.6. Conclusions

In summary, our study indicates that when the human brain is confronted by a deductive reasoning problem it engages linguistic and reasoning networks that converge across input modalities into a supramodal, language independent reasoning network. This network is temporally dynamic, with distinct brain regions being involved at different degrees during the stages of reasoning.

Current deductive reasoning theories differ in their explanation of the underlying neural computations carried out at each stage of reasoning. Unresolved questions pertain to (a) the nature of the representation of premise information, (b) whether premises are integrated into a single model and (c) how the inference process is carried out. Disentangling between neural computations for premise integration and inference process may require techniques closer to the neural signal than fMRI. Nonetheless, the present study yields insight regarding which brain regions are engaged during those processes. Regarding premise integration, mental logic theories postulate that premises are encoded independently (Braine & O'Brien, 1991; Rips, 1983), while other current theories postulate the integration of the premises into a unitary model or schema. The present study is most consistent with the conclusion that premises are integrated into a unitary supramodal model. Support for this conclusion comes from the longer reaction time to encode the second premise than to encode the first premise, and the greater BOLD signal in most areas during premise 2 encoding than during sentence 2 (control) encoding.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2008.08.030.

References

Baddeley, A. D. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience, 4*, 829–839.

Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia, 45*, 2883–2901.

Braine, M. D. (1978). On the relation between the natural logic of reasoning and standard logic. *Psychological Review, 85*, 1–21.

Braine, M. D., & O'Brien, D. P. (1991). A theory of IF: A lexical entry, reasoning program and pragmatic principles. *Psychological Review, 98*, 182–203.

Buchel, C., Price, C., & Friston, K. (1998). A multimodal language region in the ventral visual pathway. *Nature, 16*, 274–277.

Buckner, R. L., & Wheeler, M. E. (2001). The cognitive neuroscience of remembering. *Nature Reviews Neuroscience, 2*, 624–634.

Buckner, R. L. (2003). Functional-anatomic correlates of control processes in memory. *Journal of Neurosciences, 23*, 3999–4004.

Burock, M. A., Buckner, R. L., Woldorff, M. G., Rosen, B. R., & Dale, A. M. (1998). Randomized event-related experimental design allow for extremely rapid presentation rates using functional fMRI. *Neuroreport, 9*, 3735–3739.

Cabeza, R., & Nyberg, L. (2000). Neural bases of learning and memory: Functional neuroimaging evidence. *Current Opinion in Neurology, 13*, 415–421.

Chater, N., & Oaksford, M. (1999). The probability heuristics model of syllogistic reasoning. *Cognitive Psychology, 38*, 191–258.

Cheng, P. W., & Holyoak, K. J. (1985). Pragmatic versus syntactic approaches to training deductive reasoning. *Cognitive Psychology, 17*, 391–416.

Chow, H. M., Kaup, B., Raabe, M., & Greenlee, M. W. (2008). Evidence of fronto-temporal interactions for strategic inference processing during language comprehension. *Neuroimage, 40*, 940–954.

Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J. K., Holyoak, K. J., et al. (2001). Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *Neuroimage, 14*, 1136–1149.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3*, 201–215.

Dale, A. M. (1999). Optimal experimental design for event-related fMRI. *Human Brain Mapping, 8*, 109–114.

Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Jr., Redfern, B. D., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition, 92*, 145–177.

Evans, J. S., Barston, J. L., & Pollard, P. (1983). On the conflict between logic and belief in syllogistic reasoning. *Memory and Cognition, 11*, 295–306.

Evans, J. S. B. T. (2006). The heuristic-analytic theory of reasoning: Extension and evaluation. *Psychonomic Bulletin & Review, 13*, 378–395.

Fangmeier, T., Knauff, M., Ruff, C. C., & Sloutsky, V. (2006). fMRI evidence for a three-stage model of deductive reasoning. *Journal of Cognitive Neuroscience, 18*(3), 320–334.

Friston, K. J., Holmes, A. P., Poline, J. B., Grasby, P. J., Williams, S. C. R., Frackowiak, R. S. J., et al. (1995). Analysis of fMRI time-series revisited. *Neuroimage, 2*, 45–53.

Goel, V., Gold, B., Kapur, S., & Houle, S. (1997). An imaging study of deductive and inductive reasoning. *Neuroreport, 8*, 1305–1310.

Goel, V., Buchel, C., Frith, C., & Dolan, R. J. (2000). Dissociation of mechanisms underlying syllogistic reasoning. *Neuroimage, 12*, 504–514.

Goel, V., & Dolan, R. J. (2001). Functional neuroanatomy of three-term relational reasoning. *Neuropsychologia, 39*, 901–909.

Goel, V., Makale, M., & Grafman, J. (2004). The hippocampal system mediates logical reasoning about familiar spatial environments. *Journal of Cognitive Neuroscience, 16*, 654–664.

Goel, V., & Dolan, R. J. (2004). Differential involvement of left prefrontal cortex in inductive and deductive reasoning. *Cognition, 93*, B109–B121.

Gruber, O., & Goschke, T. (2004). Executive control emerging from dynamic interactions between brain systems mediating language, working memory and attentional processes. *Acta Psychologica, 115*, 105–121.

Hagoort, P. (2005). On Broca, brain and binding: A new framework. *Trends Cognition Science, 9*, 416–423.

Henle, M. (1962). On the relation between logic and thinking. *Psychological Review*, *69*, 366–378.

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, *92*, 67–99.

Hirsch, J., Rodriguez-Moreno, D., & Kim, K. H. (2001). Interconnected large-scale systems for three fundamental cognitive tasks revealed by functional MRI. *Journal of Cognitive Neurosciences*, *13*, 389–405.

Houde, O., Zago, L., Mellet, E., Moutier, S., Pineau, A., Mazoyer, B., et al. (2000). Shifting from the perceptual brain to the logical brain: The neural impact of cognitive inhibition training. *Journal of Cognitive Neurosciences*, *12*, 721–728.

Johnson-Laird, P. N., & Byrne, R. M. J. (1991). *Deduction*. Hove, United Kingdom: Erlbaum.

Johnson-Laird, P. N. (1994). Mental models, deductive reasoning and the brain. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences*. Cambridge (MA): MIT Press.

Jordan, K., Heinze, H. J., Lutz, K., Kanowski, M., & Jancke, L. (2001). Cortical activations during the mental rotation of different visual objects. *Neuroimage*, *13*, 143–152.

Knauff, M., Mulack, T., Kassubek, J., Salih, H. R., & Greenlee, M. W. (2002). Spatial imagery in deductive reasoning: A functional MRI study. *Cognitive Brain Research*, *13*, 203–212.

Knauff, M., & Johnson-Laird, P. N. (2002). Visual imagery can impede reasoning. *Memory and Cognition*, *30*, 363–371.

Knauff, M., Fangmeier, T., Ruff, C. C., & Johnson-Laird, P. N. (2003). Reasoning, models, and images: Behavioral measures and cortical activity. *Journal of Cognitive Neurosciences*, *15*, 559–573.

Lee, A. C., Robbins, T. W., Graham, K. S., & Owen, A. M. (2002). Pray or Prey?" dissociation of semantic memory retrieval from episodic memory processes using positron emission tomography and a novel homophone task. *Neuroimage*, *16*, 724–735.

Maldjian, J. A., Laurienti, P. J., Burdette, J. B., & Kraft, R. A. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage*, *19*, 1233–1239.

McDermott, K. B., Petersen, S. E., Watson, J. M., & Ojemann, J. G. (2003). A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging. *Neuropsychologia*, *41*, 293–303.

Melrose, R. J., Poulin, R. M., & Stern, C. E. (2007). An fMRI investigation of the role of the basal ganglia in reasoning. *Brain Research*, *1142*, 14–158.

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*, 1005–1016.

Newell, A., & Simon, H. A. (1972). Human problem solving. In E. A. Feigenbaum & J. Feldman (Eds.), *Computers and thought*. Englewood Cliffs, NJ: Prentice Hall.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

Osherson, D. (1975). Logic and models of logical thinking. In R. J. Famagne (Ed.), *Reasoning: Representation and process in children and adults*. Hillsdale, NJ: Erlbaum.

Osherson, D., Perani, D., Cappa, S., Schnur, T., Grassi, F., & Fazio, F. (1998). Distinct brain loci in deductive versus probabilistic reasoning. *Neuropsychologia*, *36*, 369–376.

Parsons, L. M., & Osherson, D. (2001). New evidence for distinct right versus left brain systems for deductive versus probabilistic reasoning. *Cerebral Cortex*, *11*, 954–965.

Polk, T. A., & Newell, A. (1995). Deduction as verbal reasoning. *Psychological Review*, *102*, 533–566.

Rader, A. W., & Sloutsky, V. M. (2002). Processing of logically valid and invalid conditional inferences in discourse comprehension. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*, 59–68.

Reverberi, C., Cherubini, P., Rapisarda, A., Rigamonti, E., Caltagironi, C., Frackowiak, R. S. J., et al. (2007). Neural basis of generation of conclusions in elementary deduction. *Neuroimage*, *38*, 752–762.

Rips, L. J. (1983). Cognitive processes in propositional reasoning. *Psychological Review*, *90*, 38–71.

Rips, L. J. (1994). *The psychology of proof: Deductive reasoning in human thinking*. Cambridge, MA: MIT Press.

Rodriguez-Moreno, D. (2005). *The dynamics of syllogistic reasoning: An fMRI investigation*. New York, NY: Doctoral Dissertation, Cornell University.

Schendan, H. E., Searl, M. M., Merose, R. J., & Stern, C. E. (2003). An fMRI study of the role of the medial temporal lobe in implicit and explicit sequence learning. *Neuron*, *37*, 1013–1025.

Schumacher, E. H., Laube, E., Awh, E., Jonide, J., Smith, E. E., & Koeppe, R. A. (1996). PET evidence for an amodal verbal working memory system. *Neuroimage*, *3*, 79–88.

Sloman, S. A. (1996). Individual differences in reasoning: Implications for the rationality debate. *Behavioral Brain Sciences*, *22*, 645–665.

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. *Proceedings of the National Academy of Sciences of the United States of America*, *94*, 14792–14797.

Tinaz, S., Schendan, H. E., Schon, K., & Stern, C. E. (2006). Evidence for the importance of basal ganglia output nuclei in semantic event sequencing: An fMRI study. *Brain Research*, *1067*, 239–249.

Ullman, M. T. (2004). Contributions of memory circuits to language: The declarative/procedural model. *Cognition*, *92*, 231–270.

Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory: A meta-analysis. *Cognitive, Affective and Behavioral Neuroscience*, *3*, 255–274.

Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A., et al. (1998). Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science*, *281*, 1188–1191.