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Research Report

Neural correlates of acoustic reasoning

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ABSTRACT

We report an fMRI experiment on deductive reasoning with acoustically presented problems. Twelve volunteers received problems in which an acoustic stimulus came from the left or the right of another stimulus. The participants then heard a third stimulus coming from the left or the right of one of the proceeding stimuli. Their task was to determine the spatial relation between the two stimuli they never perceived together. In the psychology of reasoning, such problems are called transitive inferences or three-term-series problems. During the early phases of the inference, activity in primary and secondary acoustic areas and in the anterior prefrontal cortex was found. Further processing was accompanied by activity in medial frontal gyrus, the cingulate cortex, and in the parietal cortex. In the final phase, activity was found in the left frontal cortex, the right cerebellum, the right superior temporal gyrus, and in the parietal lobule. These results show that different brain areas are related to different phases of an inference. Based on these findings, we propose a three-stage-model of acoustic reasoning and identify the neural structures that are involved in the cognitive processes taking place in each phase. The results also show how acoustically presented reasoning problems differ from problems in which the problems are presented visually.

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1. Introduction

During the last decade, many functional brain imaging studies have explored the neural basis of human deductive reasoning. The term “deductive reasoning” refers to the ability of humans to go beyond what is evidently given. It is an inference in which one or more propositions are true, given that other propositions are taken for granted. The propositions which are taken for granted can be verbal statements or sentences, logical expressions, or pictorial presentations. We can perceive them visually but it is also possible to receive the propositions acoustically or through any other one of our senses. It is not the input channel that matters but rather that we infer from the given propositions that other propositions must also be true.

In all of the brain imaging studies on reasoning, the reasoning materials were presented visually as sentences on a computer screen or acoustically via headphones. In these studies it was shown that reasoning with visually presented arbitrary problems involves the right hemisphere of the brain, whereas reasoning with visually presented concrete problems relies on processing in the left hemisphere (Goel and Dolan, 2001; Goel et al., 2000). During reasoning with verbally presented sentences, portions of the parieto-occipital cortices are active, pointing to the role of visuo-spatial processes (Knauff et al., 2002, 2003; Ruff et al., 2003). The more visual

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features are described in the problems, the more activity can be found in occipital cortical areas (Knauff et al., 2003). Moreover, reasoning-related activity in parietal areas correlates with visuo-spatial ability (Ruff et al., 2003; Fangmeier et al., 2006).

The main reason why the materials in all of these studies were presented as sentences is that this is the most frequent variant in our daily life. For example, in everyday conversations we draw inferences from what the other person is saying. Also, if we read a book or newspaper, we have to draw many inferences. The main disadvantage of the sentence-based research practice, however, is a confound of reasoning-related brain activity and higher-level linguistic processing. A further disadvantage of this practice is that it ignores that we often reason with non-linguistic inputs and with information that we receive more directly from our senses.

The present study is the first to explore human deductive reasoning in the acoustic domain. Imagine that you hear sound A coming from the left of another sound B and that sound B is coming from the left of sound C. From this information you can immediately draw the conclusion that sound A must be to the left of sound C. The present study mirrors exactly such inferences. All participants received spoken letters (V, X, and Z) as acoustic stimuli in a specific spatial relation. Initially they heard two stimuli one after the other from the left and the right side of the earphone. After the first pair they heard a second letter pair. The task was to determine the spatial relation between the two stimuli that had not been perceived together in the premises. This is what we refer to as *acoustic reasoning*.

We measured the brain activity of our participants by using functional magnetic resonance imaging (fMRI). The logical structure of the problems resembled the typical sentential structure used in psychological research on reasoning. In this field such problems are called *transitive inferences*, *linear syllogisms*, or *three-term-series problems* (Johnson-Laird et al., 1972; Sternberg, 1980). The two initial propositions are so-called premises, and the third proposition, which is inferred from the other two, is the conclusion.

Our materials allowed us to overcome another pitfall of earlier brain imaging studies on reasoning. In fact, all of the earlier studies examined the brain activation during the whole reasoning process in a blocked fashion, and thus could not distinguish reasoning-related processes during different stages of the reasoning process. However, from the cognitive literature on reasoning it is well known that an entire inference process can be split into three different phases. In the *premise processing phase* reasoners have to process the information given from the premises. During the *premise integration phase* the information must be integrated into one unified mental representation and a putative conclusion must be drawn. In the *validation phase*, reasoners must compare the conclusion they drew with the displayed conclusion, and indicate whether the displayed conclusion is "True" or "False".

In our experiment, we used an experimental paradigm in which we could distinguish the brain activities related to each of the three phases of an inference separately. In a second condition the participants had to simply maintain the stimuli from the premises of the identical problems in working memory without making inferences. This was done so we could distinguish the pure reasoning process from the maintenance of information in working memory.

2. Results

On the behavioral level, no difference between reasoning and maintenance problems was found. The participants gave 96% and 97% (reasoning, maintenance) correct answers. The mean response times for the reasoning and the maintenance problems were 3453 ms ($SD = 594$) and 3257 ms ($SD = 363$), respectively ($T = 1.41$; $df = 11$; $p = 0.19$). Although the reaction

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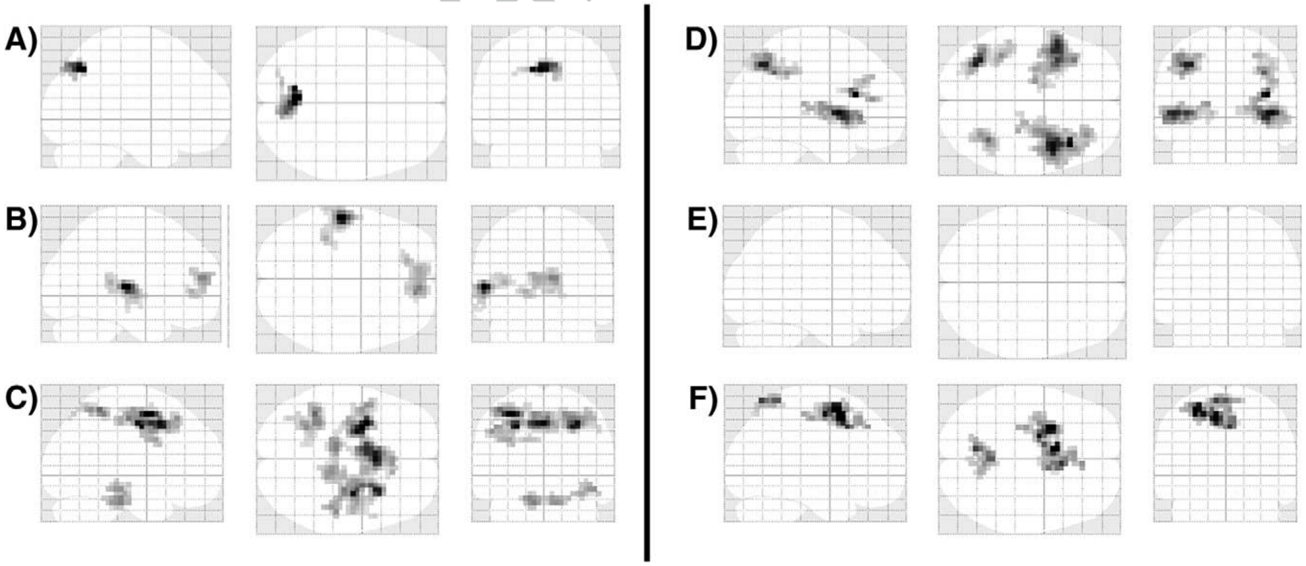

Fig. 1 – Brain activation during reasoning or maintenance problems: Reasoning problems: (A) Premise processing phase, (B) Premise integration phase, (C) Validation phase. Maintenance problems: (D) Premise processing phase, (E) Maintenance phase, (F) Validation phase. The activations were significant at the cluster level calculated with SPM5 ($p \leq .05$, corrected, threshold $t = 2.8$).

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time differences were not significant we added the reaction time as a supplementary regression parameter in the model to avoid possible effects on the resulting difference contrasts of the activity.

On the brain level, distinct patterns of activation were found for the three inference phases during the reasoning problems (Fig. 1A–C,Table 1). *The premise processing phase* activated one cluster in the medial parietal cortex (precuneus and superior parietal lobule BA 7). In the following *premise integration phase* two clusters were activated: one in the left superior temporal gyrus and parts of the left heschl gyrus (BA 41, 42), the second lay bilaterally in the superior medial frontal gyrus (BA 10) and in the left anterior cingulate cortex (BA 32). During the *premise validation phase* three clusters were found. The first cluster lay in the left middle and medial frontal gyrus (BA 6) which extended into the anterior cingulum (BA 32), the second comprised the left parahippocampal gyrus, the right cerebellum, and the right superior temporal gyrus (BA 22), and the last cluster was located in the left inferior parietal lobule (BA 40) as well as in the left superior parietal lobule (BA 7).

Table 1 – Localization of activation during the reasoning problems

Anatomical region	BA	t-score	Talairach coordinates		
			x	y	z
Premise processing phase					
Cluster medial parietal (VOX=64*)					
Precuneus (L)	7	4.73	−4	−56	43
Precuneus (L)	7	4.22	−12	−60	44
Superior parietal lobule (L)	7	3.12	−32	−64	44
Premise integration phase					
Cluster anterior prefrontal (VOX=127***)					
Medial frontal gyrus (R)	10	6.11	8	55	12
Medial frontal gyrus (L)	10	4.91	−4	55	12
Anterior cingulate cortex (L)	32	4.66	−16	43	2
Cluster left temporal (VOX=115***)					
Transverse temporal gyrus (L)	41	11.80	−55	−15	8
Heschl gyrus (L)	41	4.66	−36	−31	13
Superior temporal gyrus (L)	42	3.72	−63	−31	9
Premise validation phase					
Cluster left prefrontal (VOX=482***)					
Middle frontal gyrus (L)	6	7.33	−32	7	51
Medial frontal gyrus	6	6.18	0	14	44
Middle frontal gyrus (L)	6	6.18	−24	−2	41
Cluster midbrain (VOX=117***)					
Midbrain (L)	–	4.51	−8	−24	−19
Superior temporal gyrus (R)	22	4.19	48	−24	−9
Midbrain (R)	–	4.17	12	−28	−19
Cluster left parietal (VOX=69*)					
Inferior parietal lobule (L)	40	4.74	−40	−40	57
Postcentral gyrus (L)	40	4.39	−32	−36	53
Superior parietal lobule (L)	7	4.24	−28	−48	58

RFX-Analysis: SPM(Z)s were thresholded for height at $t=2.8$ ($df=11$), and cluster level $p\le0.05$, corrected for multiple comparisons. Locations, *t*-scores and Talairach coordinates refer to the peak voxels of the cluster. The correspondence of this voxel to Brodmann areas is only established when applicable; however note that localization can only be performed at the level of the whole cluster. VOX=number of voxels; L: left; R: right; * $p\le0.05$, ** $p\le0.01$, *** $p\le0.001$.

Table 2 – Localization of activation during the maintenance problems

Anatomical region	BA	t-score	Talairach coordinates		
			x	y	z
Premise processing phase					
Cluster right insula I (VOX=60*)					
Insula (R)	13	7.75	40	24	17
Middle frontal gyrus (R)	10	4.29	32	40	13
Middle frontal gyrus (R)	9	3.87	44	33	28
Cluster right insula II (VOX=196***)					
Insula (R)	13	6.47	44	8	3
Inferior frontal gyrus (R)	47	4.46	44	23	3
Claustrum (R)	–	3.92	28	−23	12
Cluster left insula (VOX=184***)					
Insula (L)	13	5.90	−48	12	3
Insula (L)	13	5.50	−36	12	3
Inferior frontal gyrus (L)	47	4.75	−36	27	−1
Cluster right parietal (VOX=70*)					
Inferior parietal lobule (R)	40	4.99	36	−49	39
Superior parietal lobule (R)	7	3.73	32	−56	54
Inferior parietal lobule (R)	40	3.12	40	−52	51
Cluster left parietal (VOX=140***)					
Superior parietal lobule (L)	7	5.97	−32	−60	47
Inferior parietal lobule (L)	40	4.69	−44	−52	51
Inferior parietal lobule (L)	40	4.44	−40	−37	39
Premise maintenance phase	No significant cluster				
Maintenance validation phase					
Cluster left frontal (VOX=210***)					
Middle frontal gyrus (L)	6	6.13	−28	11	55
Superior frontal gyrus (L)	6	5.63	−8	14	47
Superior frontal gyrus (L)	6	5.13	−20	−1	52
Cluster central parietal (VOX=57*)					
Precuneus (L)	7	4.57	−8	−59	66
Precuneus	7	4.36	0	−47	65
Postcentral gyrus (R)	7	3.54	12	−55	65

RFX-Analysis: SPM(Z)s were thresholded for height at $t=2.8$ ($df=11$) and cluster level $p\le0.05$, corrected for multiple comparisons. Locations, *t*-scores and Talairach coordinates refer to the peak voxels of the cluster. The correspondence of this voxel to Brodmann areas is only established when applicable; however, note that localization can only be performed at the level of the whole cluster. VOX=number of voxels; L: left; R: right; * $p\le0.05$, ** $p\le0.01$, *** $p\le0.001$. Maintenance.

The maintenance problems (Fig. 1D–E,Table 2) showed significant clusters in two phases only. In the *premise processing phase* five clusters were found: two clusters lay in the right insula (BA 13) one of them expanded into the right inferior frontal gyrus (BA 47). Another cluster lay in the left insula (BA 13) and the left inferior frontal gyrus (BA 47) and the fourth and fifth cluster covered parts of the left and right superior and inferior parietal lobule (BA 7, 40). During the *premise integration phase* no significant cluster was found. The *validation phase* activated a cluster in the left middle frontal and superior frontal gyrus (BA 6) which extended into the anterior cingulum (BA 32) as well as a cluster bilaterally in the precuneus (BA 7).

We also compared the *reasoning* and the *maintenance problems* for each of the three phases separately. Three

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activated clusters were found in which the maintenance problems showed significantly more activation during the *premise processing phase*. One cluster lay in the left superior temporal gyrus (BA 22), the second in the left posterior cingulate cortex (BA 31) and in the left paracentral lobule (BA 6, 5), and the third showed activation in the left inferior parietal lobule (BA 40), the left postcentral gyrus (BA 3), and the left precentral gyrus (BA 6).

The *reasoning problems* showed more activation during the *premise integration phase*. The cluster lay in the left insula and in the left inferior frontal gyrus (BA 47) as well as in the left precentral gyrus (BA 44). However, the cluster was not significant if we added the reaction time regression parameter ($p=0.073$), but was significant without ($p=0.042$). No difference between the two problems was found during the reasoning validation phase or the maintenance validation phase, respectively (Table 3, Fig. 2).

3. Discussion

We conducted a study in which the participants had to reason with acoustically presented stimuli and we compared the brain activation during reasoning with the activation during memory tasks in which the participants had to maintain the premises in working memory. The most fundamental result of our study is that different cortical structures are activated during different phases of deductive reasoning. Activation in superior parietal structures was found in the *premise processing phase* and activation in superior temporal gyrus, the superior medial frontal gyrus and in the cingulate cortex was found in the subsequent *integration phase*. In the *validation phase*, activation was found in the medial frontal gyrus, the parahippocampal gyrus, the cerebellum, the temporal gyrus, and in large clusters in the parietal lobules.

The maintenance problems were identical to the reasoning problems in terms of auditory input and working memory load. Here we found activation in the insula, the inferior frontal gyrus, the thalamus, and in large clusters in the superior and inferior parietal lobules during the *premise processing phase*. The *validation phase* activated clusters in the superior frontal gyrus, the left para-central lobule, and in the precuneus. Interestingly, we found no significantly elevated activity in contrast to the *integration phase*.

The direct comparison of reasoning and maintenance problems showed that overall the maintenance problems resulted in more activation during the *premise processing phase*, whereas the reasoning problems resulted in more activation in the *premise integration phase*.

The reported results have many consequences for the neuro-cognitive theory of reasoning and they also shed new light on the reasoning process under conditions where the problems are not presented as whole sentences but rather more directly as spoken letter stimuli via the auditory system. In the following, we will discuss these findings in the framework of a three-stage model of human deductive reasoning and will then compare the present findings with a very similar study in which the stimuli were presented visually. This study was recently published by Fangmeier et al. (2006).

What happens during premise processing? Here we found two large clusters of activation in the parietal cortices. The parietal cortex is supposed to play a major role in spatial processing, and in the integration of sensory information from all modalities into egocentric spatial representations (Andersen, 1997; Andersen et al., 1997; Bushara et al., 1999; Colby and Duhamel, 1996; Kolb and Wishaw, 1996; Xing and Andersen, 2000). Activation in this area is also believed to indicate the use of spatial working memory (Baker et al., 1996; Oliveri et al., 2001; Postle et al., 1999; Smith and Jonides, 1998). A recent model of the functional network underlying spatial cognition, primarily in navigation, treats parieto-occipital regions as implicated in computing head-centered representations in order to produce spatial representations of the environment, which are held in the precuneus (Burgess et al., 2001; Maguire, 2001). Previous brain-imaging studies of reasoning have similarly implied that the parietal cortex plays a key role in reasoning based on mental models, due to their abstract spatial nature (see Goel et al., 2001; Knauff et al., 2002; Knauff et al., 2003).

What happens during premise integration? Here, two different loci of activations were found. One area comprises

Table 3 – Localization of activation between reasoning and maintenance

Anatomical region	BA	t-score	Talairach coordinates		
			x	y	z
Premise processing phase					
Maintenance minus Reasoning					
Cluster temporal left (VOX=229***)					
Superior temporal gyrus (L)	22	6.55	−52	−15	5
Superior temporal gyrus (L)	22	6.16	−55	12	−1
Superior temporal gyrus (L)	22	5.34	−63	−38	9
Cluster paracentral (VOX=189***)					
Paracentral gyrus (L)	31	6.95	−4	−25	46
Paracentral gyrus (L)	6	6.16	−12	−25	49
Paracentral gyrus (R)	5	4.16	20	−33	50
Cluster pre-postcentral left (VOX=68*)					
Inferior parietal lobule (L)	40	4.71	−48	−29	46
Postcentral gyrus (L)	3	4.47	−55	−9	45
Precentral gyrus (L)	6	4.30	−44	−6	37
Reasoning minus Maintenance	No significant cluster				
Premise maintenance/integration phase					
Maintenance minus Reasoning	No significant cluster				
Reasoning minus Maintenance					
Cluster insula/ventrolateral (VOX=52$^{◆}$)					
Insula (L)	47	4.40	−32	16	−1
Inferior frontal gyrus (L)	47	3.99	−36	27	−1
Precentral gyrus (L)	44	3.56	−52	12	3
Maintenance/reasoning validation phase					
Maintenance minus Reasoning	No significant cluster				
Reasoning minus Maintenance	No significant cluster				

SPM(Z)s were thresholded for height at $t=2.8$ ($df=11$). Locations, t-scores and Talairach coordinates refer to the peak voxels of the cluster. The correspondence of this voxel to Brodmann areas is only established when applicable. VOX=number of voxels; L: left; R: right; M: medial; $^{◆}$ $p=0.073$, * $p\leq0.05$, * $p\leq0.01$, *** $p\leq0.001$, $df=11$.

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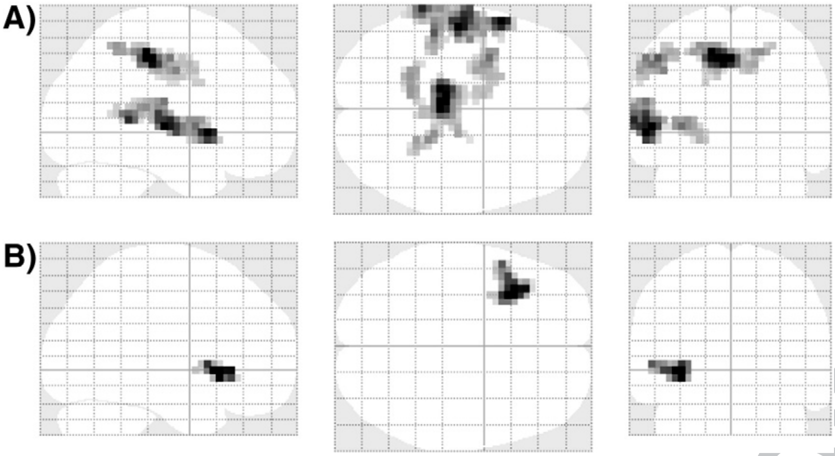

Fig. 2 – Brain activation between conditions. The figure shows differences in activation between reasoning and maintenance. Maintenance versus Reasoning: (A) premise processing phase. Reasoning versus maintenance: (B) premise integration phase. Peak voxels of the clusters in (A) were significant at the voxel level ($p \leq .05$) whereas the peak voxels in (B) were only significant without the reaction time parameters in the model (without: $p = 0.042$, number of voxels = 59; with: $p = 0.073$, number of voxels = 52). All was calculated with SPM5 with a threshold of $t = 2.8$.

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the left superior temporal gyrus and the Heschl gyrus (primary and secondary auditory cortex, BA 41, 42). These areas are typically related to the processing of auditory information (Creutzfeld, 1983; Kolb and Whishaw, 1996) and there is also evidence that the secondary acoustic areas are involved in auditory imagery (Kraemer et al., 2005; Wheeler et al., 2000; Halpern and Zatorre, 1999). Brechmann and Scheich (2005) have provided evidence for a lateralization depending on the task specificity. Some studies suggest a lateralization of the left hemisphere during working memory or auditory recall (Brechmann et al., 2007; Wheeler et al., 2000) and found that the left superior temporal gyrus is more activated during the hearing of consonants (Joanisse and Gati, 2003). Further, the left hemisphere is known as dominant for speech perception in most cases (Knecht et al., 2000). We think that the reason for the activity in the left superior temporal gyrus is that the premises must be held in auditory working memory in order to integrate them into a unified model. This activation most likely reflects a process specific to reasoning, such as premise integration. Behavioral data indicates that such integration of premise information occurs during processing of the second premise (Maybery et al., 1986). In this phase the reasoners construct *a single* integrated model of the state of affairs described in the premises, so that the premises of the reasoning problem are no longer represented as separate entities in working memory (Mani and Johnson-Laird, 1982). The activation we found is consistent with other studies that have found the area to be involved in relational integration during reasoning, or in *considering multiple relations simultaneously* (Waltz et al., 1999; Prabhakaran et al., 2000; Christoff et al., 2001; Prabhakaran et al., 2001). A review by Ramnani and Owen (2004) suggests that this area is responsible for relational integration, and the more general combination and coordination of outputs from multiple cognitive operations. In our context, it is important that we did not find a similar activation in the maintenance problems. This might reflect the fact that integration processes are necessary if participants have to reason with the premises. If, however, the participants just have to maintain the premises no such integration is necessary. Integration is only required if a conclusion must be drawn from the separate pieces of information.

What happens during the validation phase? During this phase three areas were activated. First, we found activation in the prefrontal cortex (BA 6, 8, and 32, the dorsal anterior cingulate). This activation indicates that executive processes are necessary for the control of the validation phase (Smith and Jonides, 1999; Fletcher and Henson, 2001). The main activity in the PFC lies in the middle frontal gyrus (BA 6, 8) and anatomical data show that the posterior dorsolateral prefrontal cortex BA 8A/B and rostral BA 6 have bidirectional connections with the PPC for example BA 7 and the more rostral lying DLPFC (Petrides and Pandya, 1999). We assume that this activation has to do with the variation of the model to check putative conclusions (Johnson-Laird, 1991) which was not necessary for maintenance problems.

The second locus of activation was found in the midbrain which spreads into the right parahippocampal gyrus and the right hippocampus. Activation in the right hippocampus was found during imagined or online navigation (Burgess et al., 2001; Maguire et al., 2000) and the parahippocampal gyrus was activated during object-to-place encoding (Maguire et al., 1998).

The third activation was found in the left parietal cortex. As already mentioned, this activation was often found during spatial processing and working memory tasks (Burgess et al., 2001; Oliveri et al., 2001; Postle et al., 1999; Smith et al., 1998; Q5 Baker et al., 1996). Furthermore, other studies found that in the left parietal cortex information from all modalities is integrated into a spatial representation (Xing et al., 2000; Bushara Q6 et al., 1999; Andersen et al., 1997; Colb et al., 1996). We think Q7 that this result highlights the essential role of modality-

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independent spatial representations specifically during the validation of the premises.

The question of how visual and spatial representations are involved in reasoning leads us to compare the present findings with a strongly related experiment in which the stimuli were presented visually. This study was recently published in our group (Fangmeier et al., 2006). In the study, we used an identical experimental paradigm with the same procedure, identical timing, and with the same control conditions. The only difference was that stimuli V, X, Z were presented visually on the left or on the right side of a computer screen with a back projection system.

The activations in the present experiment and the study with the visual reasoning problems have a great deal in common but there are also essential differences. In particular, in the earlier study we found activity in the visual cortices and in the temporal cortex during the premise processing phase. We argued that this shows that reasoning with materials which are easy to visualize elicit visual mental images during the processing of premises. The fact that we did not find such activity now shows that visual mental images are not essential in reasoning. They seem to serve as a tool for maintaining visually presented premises but they do not seem to be a part of the reasoning process itself.

Another difference is that we now found activation in auditory association areas. There is evidence that the secondary acoustic area is involved in auditory imagery (Kraemer et al., 2005; Wheeler et al., 2000; Halpern et al., 1999) and this might indicate that our participants now used auditory imagery as a tool to support reasoning. Presumably visual mental images (as in the earlier study) are used to maintain visually presented premises and auditory imagery (as in the present study) helps us maintain the information from acoustic presented premises. In both cases, however, the representations are not essential to the reasoning process itself, but rather are more related to the processing of the premises.

During the premise integration phase we found the same activation in the anterior prefrontal cortex in both studies. This suggests that this area is important for the integration of the two premises into one unified model. Further, we found again prefrontal cortex activation which is required for executive processes during reasoning.

The main finding in both experiments, however, was that the model variation phase consistently results in large activation clusters in the parietal cortex. This emphasizes the role of modality-independent spatial representations and processes in reasoning. Previous studies have similarly implied that the parietal cortex may play a key role in reasoning based on mental models, which are supposed to be of abstract spatial nature. However, these studies have often shown concurrent activation of visual association cortices (Goel et al., 2001; Goel et al., 2000), and interpreted that as a sign for the role of visual mental imagery in reasoning (Ruff et al., 2003; Knauff et al., 2003). The present study now shows that such activation is not present if the reasoning problems do not push reasoners towards the use of visual images.

There are several studies from outside the reasoning domain that are related to our findings. Naghavi and Nyberg (2005) in a review reported activity in fronto-parietal areas for four different research areas: attention, working memory, episodic memory and conscious perception. All of them displayed fronto-parietal activations. The authors assumed that distributed representations have to be integrated and that possible cognitive relationships of processes exist between the different research areas. Jung and Haier (2007) reviewed the human intelligence and reasoning literature and introduced a Parieto-Frontal Integration Theory (P-FIT) They assume that the integration of distributed information in the brain underlies the interaction between frontal and parietal areas.

In summary, our study on the neuro-cognitive processes underlying acoustic reasoning supports the notion that reasoning can be described as a three-stage process, reflecting premise processing, premise integration, and validation. We identified neural structures which seem specifically involved in the cognitive processes taking place in each phase. It is essential to acknowledge that this finding well agrees with two other facts: First, another study found evidence for the same three phases while the materials were quite different and the problems were presented via other perceptual systems. The corollary from these communalities is that the process of reasoning itself is a universality that works the same way in all inference processes. The second observation implies that there is a nice match between brain imaging findings and the most important cognitive theory of human reasoning. The so-called “mental models theory” relies on behavioral data only, but also assumes that reasoners construct visuo-spatial mental models, derive a putative conclusion from them, and try to validate this conclusion by searching for counter-examples contradicting this conclusion (Johnson-Laird and Byrne, 1991; Johnson-Laird, 2006). In comparison with other research domains particularly intelligence but also attention, working memory, episodic memory or consciousness there is some overlap (Jung and Haier, 2007; Naghavi and Nyberg, 2005). The chronology of the activation could appear as follows: the information is primarily stored in the domain specific areas which referred to working memory as long as it was useful. If a unified model was constructed from the two premises it is not longer helpful to store the information of the two premises in the modality-dependent visual or acoustic areas. The complete model was then stored in a more abstract spatial representation and modality-independent in the parietal cortex. For the integration of the two premises into one unified model the medial anterior prefrontal cortex was required and executive processes were mediated through the prefrontal cortex especially the anterior cinculum cortex.

Some constraints of the experiment should be noted. Only participants with good abilities for these special reasoning problems took part in our fMRI experiment (at least 75% correct answers were demanded). In addition, the sample had a normal to high visuo-constructive IQ and only male participants were tested. On account of these restrictions the results have to be interpreted in this regard. Another issue is the role of letters as non-verbal stimuli. In order to have similar stimulation in the visual (Fangmeier et al., 2006) and the acoustic domain we decided to use letters. Möttönen et al. (2006) reported that sine wave stimuli showed more activation in areas for the speech processing if they were interpreted as

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speech instead of acoustic noise. The more active area lay in the superior temporal sulcus (*x*, *y*, *z*; −61, −39, 2). In comparison to Möttönen and colleagues the activation peaks of the left temporal cluster during the integration phase lay more anterior and there was no significant cluster during the premise maintenance phase. Additionally, there is no activation in speech relevant areas during the premise validation phase which support our assumption that at the end of the reasoning process no verbal processing is necessary due to a more abstract model which was hold in the parietal cortex.

The match between neuroscientific and behavioral findings shows nevertheless how well both approaches complement each other and how both contribute to our understanding of how the mind and brain work.

4. Experimental procedures

4.1. *Participants*

Only participants who reached at least 75% correct response accuracy during a training phase outside the scanner with similar reasoning and maintenance problems took part in the study. Twelve right-handed male undergraduate and graduate students with a mean age of 22.67 (*SD* 1.78) participated in the study. Additionally, we tested their visuo-constructive ability after the MR experiment with the Block Design Test (German equivalent subtest of the Wechsler Adult Intelligence Scale, Tewes, 1991). All raw values ranged between 36 and 51 which correspond to a mean IQ of 113.75 (*SD*=11.31, range from 95 to 135). They all received a small monetary compensation. All of them had normal or corrected-to-normal vision. Informed consent was given prior to their participation in the study. None of the volunteers had any history of neurological or psychiatric disorders, or of significant drug abuse. All procedures complied with both university and hospital ethical approval.

4.2. *Materials*

All materials were presented as acoustic stimuli via noise-absorbing stereo headphones. The stimuli were small audio-files on which a male voice pronounced the letter V, X, and Z. We used the letters because we had to guarantee that the stimuli could be unambiguously identified by the participants. From these three letters, 32 *reasoning problems* were constructed. In each of the problems the stimuli were presented successively via headphones. The first premise consisted of two stimuli with one stimulus being delivered to the left ear and the other to the right ear of the participant. For instance, participants heard the V to the left and the X to the right ear. Then the second premise presented the X to the left ear and the Z to the right ear. After these premises a conclusion was presented. For instance, now the V appeared on the left side and the Z on the right side. A sentential version of this example would be: “V is to the left of X” (first premise) and “X is to the left of Z” (second premise). Does it follow “V is to the left of Z” (conclusion)? The participants had to decide whether the conclusion necessarily followed from the premises. In this example, the participants' correct response would be to conclude it is a logically valid inference. Given the two premises, the only possible inference is that the V must be to the left of the Z. Here is an illustration of a *reasoning problem* with a valid conclusion (see also Fig. 3):

Left ear	Right ear	
V	X	
X	Z	
V	Z	Yes or No?

The position (left or right) of the first term in the premises and the conclusion was changed over all problems.

Participants used an MRI-compatible response box to indicate whether the conclusion was true or false. Only the letters V, X, and Z were used because (in German) no problem-related words can be built from them.

We also used 32 *maintenance problems*. Here, the presentation of the two premises was the same as in the reasoning problems, but the participants had to decide whether the third stimulus-pair was identical (same term order) with one of the two premises. In 50% of the problems this was the case. In the other half, the stimulus-pair did not match with one of the premises. Here is an example of a valid *maintenance problem*:

Left ear	Right ear	
V	X	
X	Z	
V	X	Yes or No?

In this case, participants had to press the “Yes” key, because the third stimulus-pair is an exact replication of the first premise. Prior to each problem, the word “Schlieβen” (German equivalent for reasoning) or “Erinnern” (German for maintenance) was presented on both sides of the headphones for one second to identify the next trial as a reasoning problem or a maintenance problem, respectively. This was done because the participants should know whether they have to reason with the next problem or have to keep the premises in mind. The only difference for the problems were the different instructions for the two conditions.

Each trial began with the introduction of the nature of the stimuli (reasoning or maintenance). After a 1000 ms pause the first stimulus was presented for 1500 ms, followed by the second stimulus for 1500 ms, and a pause for 1000 ms (first premise), adding up to a total of 4 s. The time period for the second premise and the conclusion or maintenance was the same as during the first premise (1500 ms for the first letter, 1500 ms for the second letter and 1000 ms pause). Each trial lasted for about 14 s (introduction 2 s, premise 1, 2 and conclusion or maintenance 3*4 s). In half of the premises and conclusions, the stimulus to the left ear appeared first, followed by the stimulus to the right ear, whereas in the other half they were presented in the reverse order. This variation of term order is well established in reasoning research (Knauff et al., 1998) and prevented participants from recognizing the “internal logic” of the problems and from developing expectations on what followed next.

Participants responded with index and middle fingers on a response box in order to record the response times and reasoning accuracy for each problem.

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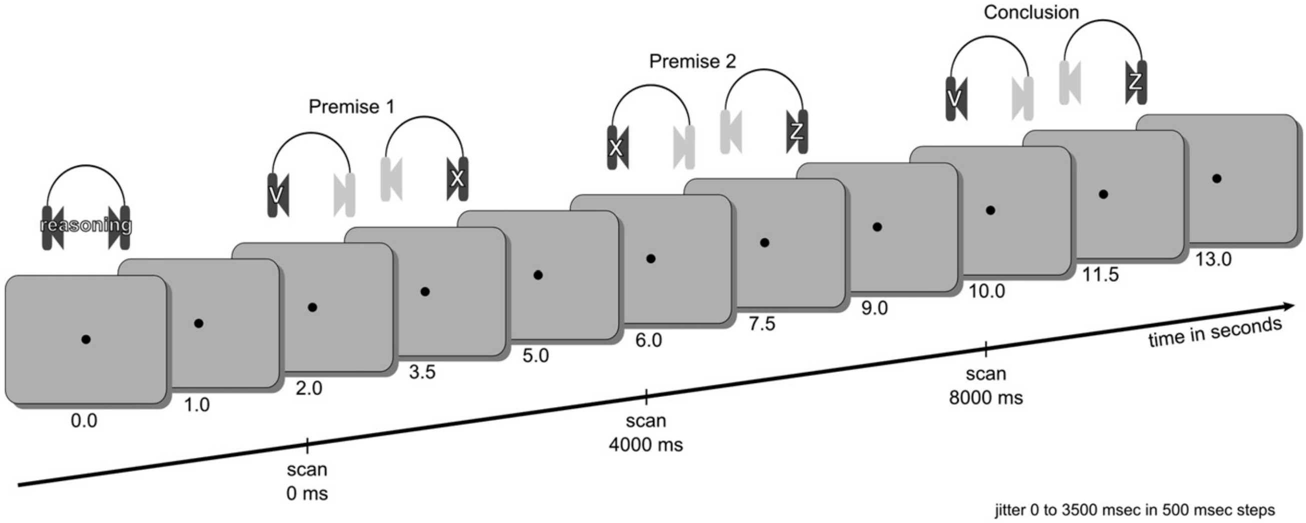

Fig. 3 – Sequence of a reasoning problem. Each problem was introduced first with the word "Schließen" (German for reasoning) or "Erinnern" (German for maintenance) via the earphones for 1 s to both ears. The spatial relation between the two letters of each premise or *conclusion* was coded by playing it on the right or on the left ear of the earphones and the auditory stimuli were spoken consonants ("V", "X", and "Z"). Each trial began with the auditory presentation of the first letter for 1500 ms, followed by the second letter for 1500 ms, and a pause for 1000 (first premise), making a total of 4 s. The time period for the second premise and the conclusion or maintenance was the same as during the first premise (total time of 14 s, 12 s for the problem plus 2 s for the introduction of the problem).

4.3. *Procedure and fMRI data acquisition*

Problems were presented in an event-related design with four separate runs. Each run contained eight reasoning and eight maintenance problems in a pseudo-randomized order. Scanning was performed on a 1.5-T Siemens Vision scanner and the participant's head was fixed in the head coil. A mirror was placed on the coil so that participants could see a projection screen mounted on the rear of the scanner bore. A fixation cross was projected on the middle of the screen using a video projector while subjects heard the problems acoustically. The participants were asked to look at the fixation cross in the middle of the screen and to not close their eyes.

The acoustic stimuli (the spoken letters V, X, and Z) were generated with a recording program. They were spoken by one of the experimenters and the volume was normalized with audio software. During the fMRI session, a pneumatic stereo headphone with a flexible tube and earplugs was used. Noise protection headphones with a hole for the flexible pneumatic tube were used in order to reduce the scanner noise.

Functional images were collected with a gradient-recalled echo-planar imaging (EPI) sequence, allowing the sampling of 30 parallel slices covering the whole brain [TR (repetition time): 4000 ms; TA (acquisition time): 3126 ms; TE (echo time): 60 ms; FOV (field of view): 256 mm × 256 mm, 4 mm × 4 mm in-plane resolution and 4 mm slice thickness; 4 mm^3 isotropic voxel size]. 114 functional image volumes were collected in each of the four stimulus runs lasting 456 s. The first two scans of each run were excluded in order for T1-effects to stabilize. A functional EPI image with 40 slices (FOV: 256 mm × 256 mm, 2 mm × 2 mm in-plane resolution and 4 mm slice thickness) and a sagittal T1-weighted magnetization prepared, rapid acquisition gradient-echo (MP-RAGE) image of the entire brain [160 slices, TR: 40 ms; TE: 6 ms; FA (flip angle): 40°; FOV: 256 mm × 256 mm, 1 mm × 1 mm in-plane resolution, and 1 mm slice thickness; 1 mm^3 isotropic voxel size] were acquired for purpose of coregistration and normalization during image preprocessing. The presentation of each stimulus (premises and conclusion) was synchronized with the TTL-pulse emitted by the scanner, and stimuli were presented with the software package "Presentation" (Presentation®, 2003).

4.4. *fMRI preprocessing*

Functional and anatomical images were reoriented so that the anterior commissure corresponded to the origin of the three-dimensional standard coordinate system used in the software Statistical Parametric Mapping 5 (SPM5, 2005). The four runs for each subject were separately realigned and corrected for motion, and underwent slice timing correction. Each subject's anatomical image was coregistered with a 40-slice EPI and the functional images of each run. The parameters for spatial normalization were determined from the anatomical images of each subject, and were applied to the corresponding functional images. Images were finally smoothed with an 8-mm full-width half-maximum Gaussian kernel.

4.5. *fMRI statistical analyses*

The hemodynamic response to the premises and conclusions was modeled with event-related delta functions, which were convolved with the canonical hemodynamic response function employed in SPM5. Low-frequency confounds were excluded from the model with a high-pass filter (192 s cutoff),

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and an autoregression AR(1) model excluded the variance explained by the previous scan. Since reaction time differences between the reasoning and maintenance problems were observed (even though they were not significantly different) we added the reaction time as an additional regression parameter for each participant and correct answer in order to control the possibility of different activation due to different latency. First-level contrast images for every subject and contrast were then used for a random effects analysis to draw inferences on brain activation during the experimental problems. Only correctly answered problems were included in the analysis.

All reported clusters within the conditions are significant at the cluster level $p \leq .05$ (instead of Fig. 1B, this cluster was only significant if we use a model without reaction time regressors), corrected for multiple comparisons (threshold $t=2.8$). The following contrasts were calculated for *reasoning*: premise processing phase (premise 1 minus premise 2), premise integration phase (premise 2 minus premise 1), validation phase (premise 2 minus conclusion). For *maintenance* the corresponding contrasts were computed: premise processing phase (premise 1 minus premise 2), maintenance phase (premise 2 minus premise 1), validation phase (premise 2 minus premise 3). The contrasts between the reasoning and maintenance conditions were: first phase (reasoning premise 1 minus maintenance premise 1), second phase (reasoning premise 2 minus maintenance premise 2), third phase (reasoning conclusion minus maintenance validation). The opposite contrasts between maintenance and reasoning were: first phase (maintenance premise 1 minus reasoning premise 1), second phase (maintenance premise 2 minus reasoning premise 2), third phase (maintenance validation minus reasoning conclusion).

5. Uncited reference

Maguire et al., 1997

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REFERENCES

Andersen, R.A., Snyder, L.H., Bradley, D.C., Xing, J., 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. Annu. Rev. Neurosci. 20, 303–330.

Baker, S.C., Frith, C.D., Frackowiak, R.S., Dolan, R.J., 1996. Active representation of shape and spatial location in man. Cereb. Cortex 6, 612–619.

Brechmann, A., Scheich, H., 2005. Hemispheric shifts of sound representation in auditory cortex with conceptual listening. Cereb. Cortex 15, 578–587.

Brechmann, A., Gaschler-Markefski, B., Sohr, M., Yoneda, K., Kaulisch, T., Scheich, H., 2007. Working memory specific activity in auditory cortex: potential correlates of sequential processing and maintenance. Cereb. Cortex 17, 2544–2552.

Burgess, N., Maguire, E.A., Spiers, H.J., O'Keefe, J., 2001. A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. Neuroimage 14, 439–453.

Bushara, K.O., Weeks, R.A., Ishii, K., Catalan, M.J., Tian, B., Rauschecker, J.P., Hallett, M., 1999. Modality-specific frontal and parietal areas for auditory and visual spatial localization in humans. Nat. Neurosci. 2, 759–766.

Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J.K., Holyoak, K.J., Gabrieli, J.D., 2001. Rostrolateral prefrontal cortex involvement in relational integration during reasoning Neuroimage 14, 1136–1149.

Colby, C.L., Duhamel, J.R., 1996. Spatial representations for action in parietal cortex. Brain Res. Cogn. Brain Res. 5, 105–115.

Creutzfeld, O.D., 1983. Cortex Ceribri. Springer, Berlin, Heidelberg.

Fangmeier, T., Knauff, M., Ruff, C.C., Sloutsky, V., 2006. FMRI evidence for a three-stage model of deductive reasoning. J. Cogn. Neurosci. 18, 320–334.

Fletcher, P.C., Henson, R.N., 2001. Frontal lobes and human memory: insights from functional neuroimaging. Brain 124, 849–881.

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

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

Halpern, A.R., Zatorre, R.J., 1999. When that tune runs through your head: a PET investigation of auditory imagery for familiar melodies. Cereb. Cortex 9, 697–704.

Joanisse, M.F., Gati, J.S., 2003. Overlapping neural regions for processing rapid temporal cues in speech and nonspeech signals. Neuroimage 19, 64–79.

Johnson-Laird, P.N., Legrenzi, P., Legrenzi, M.S., 1972. Reasoning and a sense of reality. Br. J. Psychol. 62, 395–400.

Johnson-Laird, P.N., Byrne, R.M.J., 1991. Deduction. Erlbaum, Hove (UK).

Jung, R.E., Haier, R.J., 2007. The Parieto-Frontal Integration Theory (P-FIT) of intelligence: converging neuroimaging evidence. Behav. Brain Sci. 135–154.

Knauff, M., Rauh, R., Schlieder, C., Strube, G., 1998. Mental models in spatial reasoning. In: Freksa, C., Habel, C., Wender, K.F. (Eds.), Spatial Cognition- An Interdisciplinary Approach to Representation and Processing of Spatial Knowledge. Springer-Verlag, Berlin, pp. 267–291.

Knauff, M., Mulack, T., Kassubek, J., Salih, H.R., Greenlee, M.W., 2002. Spatial imagery in deductive reasoning: a functional MRI study. Brain Res. Cogn. Brain Res. 13, 203–212.

Knauff, M., Fangmeier, T., Ruff, C.C., Johnson-Laird, P.N., 2003. Reasoning, models, and images: behavioral measures and cortical activity. J. Cogn. Neurosci. 15, 559–573.

Knecht, S., Drager, B., Deppe, M., Bobe, L., Lohmann, H., Floel, A., Ringelstein, E.B., Henningsen, H., 2000. Handedness and hemispheric language dominance in healthy humans. Brain 123, 2512–2518.

Kolb, B., Whishaw, I.Q., 1996. Neuropsychologie. Spektrum, Akad. Verl., Oxford.

Kraemer, D.J.M., Macrae, C.N., Green, A.E., Kelley, W.M., 2005. Musical imagery: sound of silence activates auditory cortex. Nature 434, 158.

Maguire, E.A., Frackowiak, R.S., Frith, C.D., 1997. Recalling routes around London: activation of the right hippocampus in taxi drivers. J. Neurosci. 17, 7103–7110.

Please cite this article as: Fangmeier, T., Knauff, M., Neural correlates of acoustic reasoning, Brain Res. (2008), doi:10.1016/j.brainres.2008.10.025

Maguire, E.A., Burgess, N., Donnett, J.G., Frackowiak, R.S., Frith, C. D., O'Keefe, J., 1998. Knowing where and getting there: a human navigation network. Science 280, 921–924.

Maguire, E.A., Gadian, D.G., Johnsrude, I.S., Good, C.D., Ashburner, J., Frackowiak, R.S., Frith, C.D., 2000. Navigation-related structural change in the hippocampi of taxi drivers. Proc. Natl. Acad. Sci. U. S. A. 97, 4398–4403.

Mani, K., Johnson-Laird, P.N., 1982. The mental representation of spatial descriptions. Mem. Cogn. 10, 181–187.

Maybery, M.T., Bain, J.D., Halford, G.S., 1986. Information-processing demands of transitive inference. J. Exper. Psychol. Learn. Mem. Cogn. 12, 600–613.

Möttönen, R., Calvert, G.A., Jääskeläinen, I.P., Matthews, P.M., Thesen, T., Tuomainen, J., Sams, M., 2006. Perceiving identical sounds as speech or non-speech modulates activity in the left posterior superior temporal sulcus. Neuroimage 30, 563–569.

Naghavi, H.R., Nyberg, L., 2005. Common fronto-parietal activity in attention, memory, and consciousness: shared demands on integration? Conscious. Cogn. 14, 390–425.

Oliveri, M., Turriziani, P., Carlesimo, G.A., Koch, G., Tomaiuolo, F., Panella, M., Caltagirone, C., 2001. Parieto-frontal interactions in visual-object and visual-spatial working memory: evidence from transcranial magnetic stimulation. Cereb. Cortex 11, 606–618.

Postle, B.R., Berger, J.S., D'Esposito, M., 1999. Functional neuroanatomical double dissociation of mnemonic and executive control processes contributing to working memory performance. Proc. Natl. Acad. Sci. U. S. A. 96, 12959–12964.

Prabhakaran, V., Narayanan, K., Zhao, Z., Gabrieli, J.D., 2000. Integration of diverse information in working memory within the frontal lobe. Nat. Neurosci. 3, 85–90.

Prabhakaran, V., Rypma, B., Gabrieli, J.D., 2001. Neural substrates of mathematical reasoning: a functional magnetic resonance imaging study of neocortical activation during performance of the necessary arithmetic operations test. Neuropsychology 15, 115–127.

Presentation®, 2003. Computer Software. Neurobehavioral Systems, Albany (USA, CA).

Ramnani, N., Owen, A.M., 2004. Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. Nat. Rev. Neurosci. 5, 184–194.

Ruff, C.C., Knauff, M., Fangmeier, T., Spreer, J., 2003. Reasoning and working memory: common and distinct neuronal processes. Neuropsychologia 41, 1241–1253.

SPM5, 2005. Computer Software. Wellcome Department of Cognitive Neurology, London (UK).

Smith, E.E., Jonides, J., 1998. Neuroimaging analyses of human working memory. Proc. Natl. Acad. Sci. U. S. A. 95, 12061–12068.

Smith, E.E., Jonides, J., 1999. Storage and executive processes in the frontal lobes. Science 283, 1657–1661.

Sternberg, R.J., 1980. Representation and process in linear syllogistic reasoning. J. Exp. Psychol. 109, 119–159.

Tewes, R., 1991. Hamburg-Wechsler-Intelligenztest für Erwachsene [German version of the WAIS-R]: revision 1991, 2nd, corrected ed. Hogrefe Publishers, Göttingen (Germany).

Waltz, J.A., Knowlton, B.J., Holyoak, K.J., Boone, K.B., Mishkin, F.S., Menezes Santos, M.d., Thomas, C.R., Miller, B.L., 1999. A system for relational reasoning in human prefrontal cortex. Psychol. Sci. 10, 119–125.

Wheeler, M.E., Petersen, S.E., Buckner, R.L., 2000. Memory's echo: vivid remembering reactivates sensory-specific cortex. Proc. Natl. Acad. Sci. U. S. A. 97, 11125–11129.

Xing, J., Andersen, R.A., 2000. Models of the posterior parietal cortex which perform multimodal integration and represent space in several coordinate frames. J. Cogn. Neurosci. 12, 601–614.

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Please cite this article as: Fangmeier, T., Knauff, M., Neural correlates of acoustic reasoning, Brain Res. (2008), doi:10.1016/j.brainres.2008.10.025