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The Neural Mechanisms of Relational Reasoning: Dissociating Representational Types

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Abstract

The ability to reason about information is an essential human capability. It is less understood from the perspective of neuro-cognitive processes which can serve to constrain cognitive theories by implications from neuroscientific data. Despite some progress in the last decades, some disagreement about the experimental results and the cognitive processes of reasoning with abstract relations versus visuospatial relations persist. We conducted a cross-study meta-analysis of neuroimaging studies to determine the neural correlates of visuospatial and abstract relational reasoning. We analyzed 884 stereotactic data points from 38 studies and 692 subjects. We found that relational reasoning is mediated by the fronto-parietal network, especially the right precuneus and the left pars triangularis. Problems with abstract relations are processed by enhanced activation in the inferior parietal lobe, whereas visuospatial reasoning is promoted by prefrontal domains. Our results disentangle the neurocognitive mechanisms of different representational types of relational reasoning across study designs.

Keywords: meta-analysis; fMRI; reasoning; relational reasoning; analogical reasoning; mental representation, precuneus, pars triangularis

Introduction

Relational reasoning expedites human everyday life to a great extent. Using relational expressions can decrease the number of statements we would need otherwise to describe the situation. If we want to 'decompress' this information, we draw inferences from the given information to extract what is implicitly present. For example, suppose you are visiting London for the first time and you want to visit London Eye. You take the underground, arrive at Waterloo Station and ask a fellow passenger for the directions. She tells you that the London Eye is behind Jubilee Gardens which are, from your perspective, in front of Waterloo Station. Due to this description, you can easily find your goal destination. But how would you find your way from the station to London Eye without having any explicit information about the spatial orientation? You do need to reason, that means, you need to extract the information from the two statements by inferring that the London Eye is located behind the train station.

Reasoning has been subject to neurocognitive research for the past thirty years. With the advent of neuroimaging methods such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) in the late 1990s and early 2000s, seminal work has been accomplished by investigating the neural correlates of reasoning (Prado, Chadha & Booth, 2011). The potential for research in relational reasoning is manifold. For instance, Knauff and Johnson-Laird (2002) proposed to differentiate deductive relational reasoning tasks based on the kind of mental representation necessary to represent relations. They established the categories of visual, spatial and visuospatial mental representation of the relations which differs from the mental representation of objects they relate. For our study, we decided to reevaluate the differentiations and employed new definitions for the types of mental representation. A relation helps to structure human experiences about one or many objects in everyday life and they can be of different types. A *spatial* relation reflects implicitly or explicitly an order of objects (e.g., the apple is to the left of the pear). Such a relation can be perceived by the visual system and additionally by other sensory systems that allow to perceive order such as 'touch' for instance. A pure *visual* relation in turn is only perceivable by the visual system and by no other perception system (e.g., the grass is greener than the tree). *Visuospatial* relations are perceivable by both, the visual and other systems, such as 'laying on top of something' – this is an ordered relation and at the same time the relation 'top' presupposes a surface perceived *visually*. *Abstract* relations are inconceivable by any sensory systems, such as mental attributions (e.g., smarter than) or abstract mathematical operations (e.g., '=').

To the best of our knowledge, there is currently no study investigating such aspects of relational reasoning that directly relate to different degrees of imaginability of relations. To collect a sufficient number of data by often diverse study designs, we decided to use a broader, more inclusive relaxation on the data aggregation. Such a relaxation on the rather strict definitions is necessary since methods such as activation likelihood estimation (ALE) are more accurate for larger datasets (Eickhoff et al., 2016).

On the basis of this experimental background, we decided to investigate relational reasoning in general as well as two of its variants, visuospatial and abstract relational reasoning. Our hypotheses are: (1) For the abstract condition, we expect enhanced activation in the posterior parietal cortex (PPC) (Hobeika, Diard-Detoeuf, Garcin, Levy & Volle, 2016; Maier, Ragni, Wenczel & Franzmeier, 2014; Wendelken 2015) and the rostrolateral prefrontal cortex (RLPFC) which are regions known to be involved in the processing of abstract information (Christoff, Ream, Geddes & Gabrieli, 2003). (2) We expect activation in the right superior parietal lobule (SPL) for the visuospatial condition. This is because it is hypothesized that visuospatial mental representations in reasoning are constructed and maintained by the help of these regions (Maier et al., 2014; Ragni, Franzmeier, Maier & Knauff, 2016).

To study the neural correlates of relational reasoning we considered 38 experiments with a total of 692 participants and 884 foci to find the neural sites which are most likely to be active during relational reasoning in general and in visuospatial and abstract relational reasoning. The results are interpreted in the light of prior neurocognitive research.

Table 1: Overview of the experiments included in the meta-analysis with details about the experimental setup.

Publication	Foci	Subj.	Rep.	Stim.
Goel et al., 1998	6	12	vs	v, sen
Goel & Dolan, 2001	36	14	vs, ns	v, sen
Christoff et al., 2001	7	10	vs	v, sha
Prabhakaran et al., 2001	202	7	ab	v, sen
Knauff et al., 2002	16	12	vs	aud, sen
Acuna et al., 2002	17	15	vs	v, sha
Knauff & Johnson-Laird, 2002	2	12	v/v, s	aud, sen
Knauff et al., 2003	28	12	vs, v, s, ab	aud, sen
Ruff et al., 2003	20	12	vs	aud, sen
Goel et al., 2004	19	14	s	v, sen
Fangmeier et al., 2006	36	12	vs	v, let
Green et al., 2006	2	14	ab	v, wor
Lee et al., 2006	8	36	vs	v, sha
Melrose et al., 2007	14	19	v, s	v, sha
Wendelken et al., 2008	24	20	ab	v, wor
Eslinger et al., 2009	17	16	vs	v, sha
Fangmeier & Knauff, 2009	21	12	vs	aud, let
Goel et al., 2009	10	17	v	v, sen
Prado, Noveck et al., 2010	3	15	vs	v, sen
Wendelken & Bunge, 2010	17	16	vs	v, sha
Prado, van der Henst et al., 2010	7	13	vs	v, sen
Hinton et al., 2010	2	24	v	v, let
Cho et al., 2010	9	17	v	v
Hampshire et al., 2010	15	16	ab	v, sha
Preusse et al., 2010	8	17	vs	v, sha
Volle et al., 2010	68	16	vs	v, let
Preusse et al., 2011	6	40	vs	v, sha
Jia et al., 2011	39	20	ab	v
Brzeziczka et al., 2011	40	17	ab	v, let
Prado et al., 2012	3	30	v	v, sen
Shokri-Kojori et al., 2012	20	20	vs	v, sha
Watson & Chatterjee, 2012	3	23	vs	v, sha
Kalbfleisch, 2013	21	34	vs	v, sha
Bazargani et al., 2014	12	37	v	v, sha
Liang et al., 2014	24	23	ab	v, let
Parkin et al., 2015	53	20	vs	v, sha
Jia et al., 2015	24	15	ab	v, num
Jia & Liang, 2015	21	13	ab	v, num

Abbreviations: Subj.: Number of subjects, Rep.: Representation type, Stim.: Stimulus, vs: visuospatial, v: visual, ns: nonspatial, ab: abstract, spa: spatial, sen: sentence, aud: auditory, sha: shapes, let: letters.

Methods

We apply the ALE method (Eickhoff, Bzdok, Laird, Kurth & Fox, 2012) which has become a standard to conduct meta-analyses to investigate neural correlates (e.g., Hobeika et al., 2016). We include as neuroimaging methods functional magnet resonance imaging (fMRI) and positron emission tomography (PET) data.

Paper Acquisition and Selection

For acquiring neuroimaging data, we conducted several online search queries via the online platforms PubMed, ScienceDirect and Google Scholar to find peer-reviewed fMRI and PET studies (see Table 1) between 1998 and 2017. We used the search terms ‘fMRI OR PET OR Neuroimaging’, ‘relational OR transitive reasoning’ and ‘visual reasoning OR spatial reasoning OR visuospatial reasoning’ in all queries and additionally for the query in Science direct ‘healthy’, and for Google Scholar ‘MNI OR Talairach’. Additional articles were found via the reference lists of similar papers, the meta-analysis conducted by Prado, Chadha and Booth (2011) and the reviews by Knauff (2006) and Maier et al. (2014). Due to a review of the meta-analysis conducted by Prado, Chadha and Booth (2011), ‘reasoning vs. baseline’ conditions (such as fixation cross or maintenance tasks, see e.g., Wendelken, Nakhabenko, Donohue, Carter & Bunge, 2008 and Ruff, Knauff, Fangmeier & Spreer, 2003, respectively) as well as ‘high- vs. low-level reasoning’ conditions were included since they represent an aspect of reasoning. Additionally, experimental data were only included when they were reported in MNI or Talairach space and yielded from whole brain analyses.

Paper Categorization

We decided to categorize the data along different axes: by the type of mental representation of the relation (abstract, spatial, visual, visuospatial, none), by the stimulus (letters, sentences, shapes, words, numbers) and the type of stimulus presentation (visual or auditory) (see Tables 1 and 2). We acknowledge that these differences may reflect differences in neural activation as well but chose to only consider the types of mental representation and subtraction for the sake of including more studies in each group and yielding more robust results.

When reviewing the articles, we realized that our definitions for the mental representations of relations did not fit to what can be found in actual studies. Because of that, we decided to lower our criteria so that we merged the groups ‘visual’, ‘spatial’ and ‘visuospatial’ to the group ‘visuospatial’ (see Table 2). Also, we redefined the criteria so that visuospatial relations are relations that are easy to mentally envision in a spatial and/or visual manner in the aforementioned sense. For abstract tasks, we included all tasks that are impossible to potentially perceive by senses, such as mathematical tasks and operators (e.g., ‘=’, ‘<’, ‘>’).

Activation Likelihood Estimation

ALE is an established method for conducting meta-analyses of neuroimaging data (Eickhoff et al., 2012). It is implemented in the statistical tool GingerALE[1] (we used version 2.3.6) to determine the likelihood of individual brain regions activating for a specific task. GingerALE features the conduction of either single dataset analyses or conjunction and contrast analyses between datasets.

The ALE algorithm maps the stereotactic data of each experiment on a template brain to generate Modeled Activation (MA) maps. Since the reported data are as points, it reconstructs the scanning data by assigning each data point the center of a Gaussian distribution. The points are blurred by the full width at half maximum (FWHM) which is determined by the subject size of the respective dataset (Eickhoff et al., 2012). The MA maps are merged to render the final ALE file. For each voxel, the likelihood confidence of finding each value is calculated by neglecting spatial information from the dataset and analyzing the probabilities of values being part of an MA map. The information from the two files is combined and a threshold is applied to constitute the final ALE map (Eickhoff et al., 2012). In our analysis, we chose a standard setting of 1000 permutations, the cluster-level family-wise error (FWE) method with a *p*-value of 0.01 and an uncorrected *p* of 0.001 (Eickhoff et al., 2016). The cluster-level FWE method generates a random dataset tantamount to the set at hand (regarding subject size, number of foci and number of studies) which is compared to the actual data set. Foci originally represented in MNI (Montreal Neurological Institute) space were converted to Talairach space. In conjunction and contrast analyses, the ALE maps of two sets are examined in activation likelihood for their overlap and distinctness respectively.

Table 2: Details of the paper categorizations with regard to the quantitative parameters of the groups.

Representation	**Studies**	**Subjects**	**Foci**
all	38	692	884
abstract	10	179	394
spatial	2	16	23
visual	8	161	47
visuospatial	28	521	445
none	2	26	23

Results

Relational Reasoning

For the relational reasoning condition, activation was most likely found in the right precuneus (BA 7) and the left middle occipital gyrus (BA 31). Concerning the frontal lobe, the left inferior frontal gyrus (pars triangularis), left posterior-medial frontal, left and right middle frontal gyrus (BA 6) and the left middle orbital gyrus (BA 46) were found. Additionally, activation was found in the right basal ganglia (Tables 3 and 4).

Table 3: Overview of brain activation

	Frontal				Parietal		S	O
	46	6	44	45	7	40	13	31
Relational	◖	◐		◖	◗		◗	◖
Visuospatial		◐	◖	◗	◐			
Abstract					◗	◖		

Note. Semicircles indicate significant clusters in the respective hemisphere. Filled halves indicate that the respective side’s cluster was larger in this half. Abbreviations: S: Sub-Lobar, O: Occipital.

Reasoning with Visuospatial Relations

In the visuospatial condition, activation was most likely in the left inferior frontal gyrus (triangularis, BA 44), posterior-medial frontal (BA 6), right and left middle frontal gyrus (BA 6) and the left inferior parietal lobule (hIP3, BA 7) and right superior parietal lobule (BA 7A).

[1] http://www.brainmap.org/ale/

Reasoning with Abstract Relations

Activation in reasoning about abstract relations was found in the right angular gyrus and left superior parietal lobule (hIP 1/3 respectively, both BA 7) and the left and right inferior frontal gyrus (triangularis, BA 45) and precentral gyrus (BA 45).

Table 4: ALE Results. Only significant clusters and a differentiated anatomical localization is reported.

Macroanatomical Location		BA	Coordinates (Tal)		
			X	Y	Z
Relational Reasoning Inference					
R	Precuneus	7	0	-61	43
L	IFG (p. Triangularis)	45	-45	13	32
L	Posterior-Medial Frontal	6	-1	11	48
R	IFG (p. Triangularis)	9	45	18	32
L	Middle Frontal Gyrus	6	-27	0	53
R	Middle Frontal Gyrus	6	28	-1	52
R	Basal Ganglia	13	27	23	3
L	Middle Orbital Gyrus	46	-41	43	6
L	Middle Occipital Gyrus	31	-27	-77	25
Relational Reasoning abstract					
R	Angular Gyrus	7	23	-65	42
L	Superior Parietal Lobule	7	-26	-65	44
L	IFG (p. Triangularis)	45	-44	23	26
L	Precentral Gyrus	44	-43	3	33
Relational Reasoning visuospatial					
L	IFG (p. Triangularis)	44	-46	12	33
L	Posterior-Medial Frontal	6	-1	12	47
L	Inferior Parietal Lobule	7	-35	-55	44
R	Middle Frontal Gyrus	6	28	-1	53
L	Middle Frontal Gyrus	6	-26	-1	56
R	IFG (p. Triangularis)	45	46	25	33
R	Superior Parietal Lobule	7	23	-65	44

Abbreviations: BA: Brodmann Area, IFG: Inferior Frontal Gyrus.

Discussion

Relational Reasoning involves the fronto-parietal network and occipital lobe

For reasoning about relations, we found activation likelihood in the fronto-parietal network (right pars triangularis, posterior-medial frontal lobe, middle frontal gyrus, precuneus, left dorsolateral prefrontal cortex (DLPFC) and pars triangularis). These results are in accordance with the activation detected in the studies by Hobeika et al. (2016) and Prado, Chadha and Booth (2011). The largest cluster was found in the right precuneus (16800 mm^3). The weighted center of this cluster is located in the frontal precuneus which is assumed to be involved in mental imagery (Cavanna & Trimble, 2006). The second largest cluster (6256mm^3) was found in the left pars triangularis, also known as DLPFC. It is known to be involved in working memory and relational integration (Waltz et al., 1999), as well as speech and language production (Foundas, Eure, Luevano & Weinberger, 1998)

Furthermore, activation was found in the right basal ganglia (BA 13), which are involved in reasoning and rule application (Melrose, Poulin & Stern, 2007), a demand inductive reasoning tasks pose. Additionally, activation was found in the occipital lobe (left middle occipital gyrus). Prado, Chadha and Booth (2011) did not find such activation for relational reasoning, though they only considered deductive reasoning tasks. This reliable activation pattern might be due to the portion of tasks with visual contents which are not considered classical deduction tasks. In contrast to Prado, Chadha and Booth (2011), Hobeika et al. (2016) and Wendelken et al. (2008), we did not find any activation of the RLPFC. A rather surprising result when considering the consistent reports thereof in the literature.

Visuospatial relational processing is executed by prefrontal activation

In visuospatial relational reasoning, the fronto-parietal network exhibited activation as well. Activation was mainly found in the left pars triangularis (BA 44) and posterior medial frontal (BA 9) and the inferior parietal lobule (hIP3) and right middle frontal gyrus (BA 45). This suggests that visuospatial relational reasoning is rather mediated by prefrontal activation, considering the multitude of clusters across the PFC. Also, parietal activation in the inferior parietal lobule (IPL) was found, suggesting that visuospatial processing does more heavily rely on context related processes than on mental imagery.

Abstract relational reasoning relies on the intraparietal sulcus

In the abstract reasoning condition, we found activation in the right intraparietal sulcus (IPS) and left IPL. Since the analysis consisted of 10 studies only, the results are sparse. Nonetheless, they indicate that the IPL is essential for abstract relational reasoning. Since the IPL is known to be involved in abstraction (Wurm & Lingnau, 2015), this might imply the IPL's crucial role in the abstraction of contents from relational information.

Conclusion

The meta-analysis unraveled some crucial details about the neural mechanisms of relational reasoning. Our results suggest that relational reasoning heavily relies on mental imagery and representation as well as a multitude of regions in the prefrontal cortex such as the DLPFC for relational integration and pars triangularis for language processing. No significant activation in the RLPFC was found, opposed to predictions by previous studies. We found striking differences between the type of representation of relations, so that visuospatial relations seem to rather rely on context, opposed to abstract relations which rely on abstraction of relation and mental imagery. Since the inclusion criteria concerning stimulus presentation and task requirements were relaxed, we assume that these areas mediate the general process of relational reasoning.

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