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Self-similarity and recursion as default modes in human cognition

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ABSTRACT

Humans generate recursive hierarchies in a variety of domains, including linguistic, social and visuo-spatial modalities. The ability to represent recursive structures has been hypothesized to increase the efficiency of hierarchical processing. Theoretical work together with recent empirical findings suggests that the ability to represent the self-similar structure of hierarchical recursive stimuli may be supported by internal neural representations that compress raw external information and increase efficiency.

In order to explicitly test whether the representation of recursive hierarchies depends on internalized rules we compared the processing of visual hierarchies represented either as recursive or non-recursive, using task-free resting-state fMRI data. We aimed to evaluate the relationship between task-evoked functional networks induced by cognitive representations with the corresponding resting-state architecture. We observed increased connectivity within Default Mode Network (DMN) related brain areas during the representation of recursion, while non-recursive representations yielded increased connectivity within the Fronto-Parietal Control-Network.

Our results suggest that human hierarchical information processing using recursion is supported by the DMN. In particular, the representation of recursion seems to constitute an internally-biased mode of information-processing that is mediated by both the core and dorsal-medial subsystems of the DMN. Compressed internal rule representations mediated by the DMN may help humans to represent and process hierarchical structures in complex environments by considerably reducing information processing load.

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1.   Introduction

The ability to understand and generate complex hierarchical structures is a hallmark trait of human cognition. The investigation of the neural bases of hierarchical processing is thus essential to understand the foundations of human cognitive architecture.

Recursion is a cognitive faculty postulated to play a significant role in human hierarchical processing (Corballis, 2011; Fitch, 2010; Hauser, Chomsky, & Fitch, 2002). In particular, recursion is thought to be necessary to achieve infinite use of finite means, and hypothesized to be available exclusively to humans (Fitch, Hauser, & Chomsky, 2005; Hauser et al., 2002). A simple example of a recursive process is the generation of natural numbers using the formula $N_i = N_{i-1} + 1$, in which both sides of the "transformation" rule contain elements belonging to the category "N". This simple process allows the generation of the infinite set of natural numbers.

Recursion can be used to generate both hierarchical and non-hierarchical structures. However, infinite 'flat' sequences without hierarchy can also be generated using simple non-recursive processes. Parsing such 'flat' structures is achievable by non-human animals (Fitch & Friederici, 2012; Nelson, Conway, & Christiansen, 2001 for reviews), and it can be difficult to distinguish, from behavioral data, whether recursive or non-recursive processes were used. Because of these empirical difficulties and because humans are especially sophisticated in their ability to handle hierarchies (as in language, music and action sequencing), a core research focus concerning recursion investigates how it enhances the processing of hierarchical structures.

Hierarchies are tree-like organizations, where higher levels incorporate multiple lower levels in structural representations (Fitch & Martins, 2014). Tree-like organizations are common in nature and in the human environment (Fig. 1), and having the cognitive resources available to represent them can enable multiple useful behaviors. For instance, an individual able to represent the hierarchical structure of a social group will have obvious generalization advantages over an individual unable to represent the same group as hierarchically organized. In the same vein, an individual able to represent appropriate hierarchies as recursive (Fig. 2) will have advantages over individuals unable to project recursive structures to new hierarchical levels (Martins, Muršič, Oh, & Fitch, 2015; Martins, 2012). In particular, being able to represent the similarity between different levels of a hierarchy (hierarchical self-similarity) allows the use of this representation to extend the hierarchy to further levels beyond the given (Martins, 2012). In other words, representing hierarchical self-similarity affords the ability to build hierarchies of unlimited depth. Even if the depth is limited by performance and memory constraints, this kind of flexible representation would still be advantageous when parsing complex hierarchies with cross-level similarities such as in visual perception, music, language, theory of mind, complex action, mathematics and architecture (Eglash, 1997, 1998; Eisenberg, 2008; Friederici, Bahlmann, Friedrich, & Makuuchi, 2011; Friedrich & Friederici, 2009; Jackendoff & Lerdahl, 2006; Janszky,

Mertens, Janszky, Ebner, & Woermann, 2006; Martins, 2012; Miller, 2009; Pinker & Jackendoff, 2005, Fig. 2).

Evidently, not all hierarchies exhibit this kind of self-similar structure, and humans use both recursive and non-recursive representations to generate and parse hierarchies. The interesting question is not whether humans *always* use recursive representations, but whether these are *available* to our cognitive apparatus, and how they are instantiated. Crucially, there is no inconsistency between the view that humans are sensitive to recursive structures, but can also process non-recursive structures, i.e., that some cognition is recursive and some cognition not. The core of the paradigm that we use in this experiment is the comparison between recursive and non-recursive representations of the same fractal stimuli (Martins, Fischmeister, et al., 2014). Thus, both our framework and our experiment are compatible with the view that humans are sensitive to both recursive and non-recursive rules.

It is important to note and forestall a potential formal criticism of our approach here: that mathematical proofs concerning recursion make crucial use of infinite sets, but our conceptual and empirical framework makes no mention of infinity. This is because one can never, in reality, observe infinite sets, or expect humans to produce infinite numbers of sentences. Our central goal in this research program is to devise empirical tests for recursive abilities in different cognitive domains, and to understand the neural bases of such abilities. To accomplish this, we perforce rely on behavioral output which indicates one of the core properties of recursion: self-embedding. A mathematician might complain that, even by showing multiple levels of self-embedding, we have not "proven" recursion, because we cannot show that such embedding could go on forever. But this is equally true of ANY psychological evaluation: if we test a subject on addition and they correctly add together 100 pairs of random integers, we conclude that they can add integers — even if they haven't demonstrated an ability to add all possible integers. We see our focus on an empirically-evaluated ability to correctly process self-embedded structures as analogous, and interpret our results as solid evidence for recursive abilities; even though we do not test whether (or claim that) our participants can process infinite-depth structures. Any definition of recursion which relies on infinity as its *sine qua non* is, by definition, empirically untestable. A similar approach has been used by other authors (e.g., Moro, 2015 for a review).

Recursion, understood as a cognitive ability useful for the generation of complex hierarchies, was first thought to be language domain-specific (Hauser et al., 2002), and most of the available theoretical and empirical work has focused on this domain. However, recent research has shown that both human adults and children are able to represent hierarchies using recursion in the visuo-spatial domain (Martins, Laaha, Freiberger, Choi, & Fitch, 2014). This capacity is independent of verbal resources (Martins et al., 2015) and does not recruit classical perisylvian language areas in the brain (Martins, Fischmeister, et al., 2014).

The independence of visual recursion from verbal resources and language brain areas suggests that the instantiation of recursion in vision partially depends on different cognitive and neural resources than in language. For

A) Linguistic syntax hierarchy

B) Social hierarchy

C) Action sequencing hierarchy
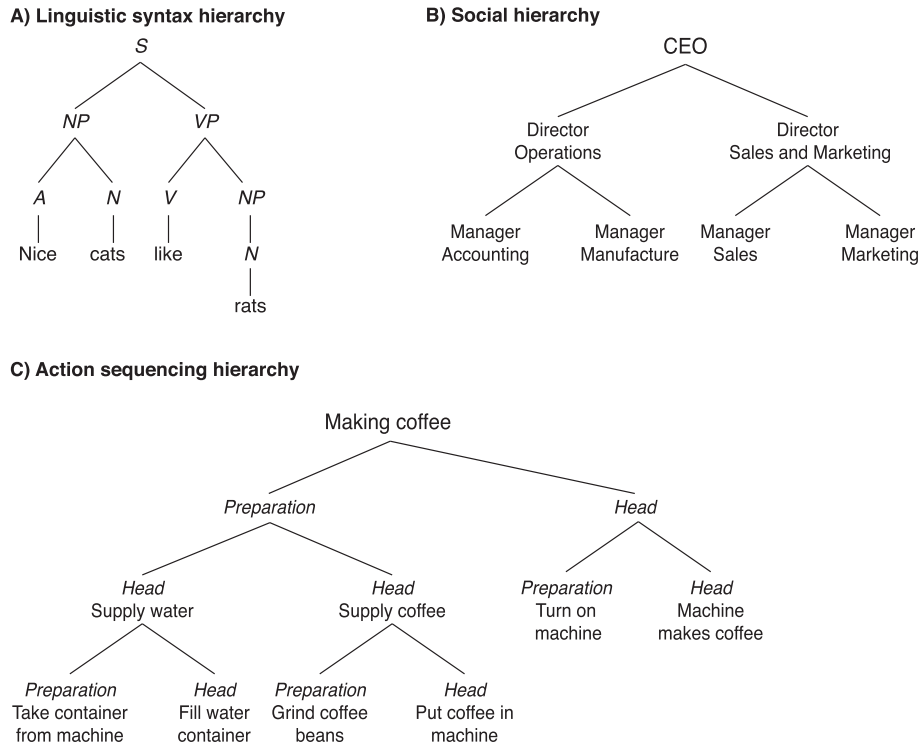
Fig. 1 − **Examples of linguistic (A), social (B) and action sequencing (C) hierarchies.**

instance, some aspects of language recursion, such as serial order and phonological constraints do not apply to the visuo-spatial domain. However, these specific constraints might be either part of the core capacity of language recursion *per se* or part of the interfaces between recursion and other systems (e.g., phonological), which are necessary for the externalization of language (Hauser et al., 2002). These leaves open the question of (1) whether visual and

A) Syntactic recursion: Embedding of a noun phrase (NP) inside another noun phrase.
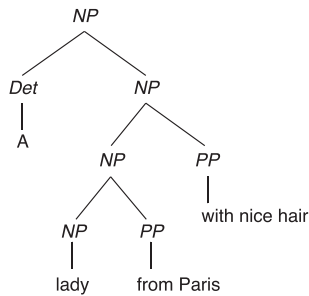
B) Social recursion: Add two 'Company Y' members as subordinates of another 'Company Y' member.
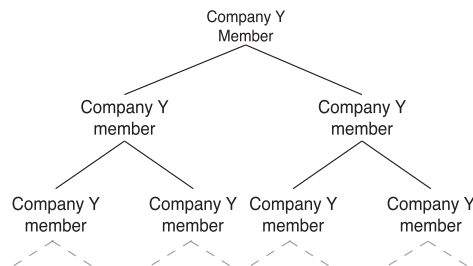
C) Visuo-spatial recursion: Add five smaller hexagons around each bigger hexagon.
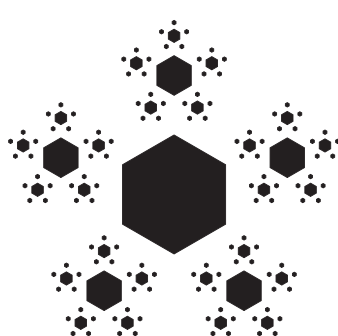
D) Recursive mental states: 'Mary thinks that John is thinking about her'.

Fig. 2 − **Examples of structures that can be efficiently represented using recursive rules.**

language recursion share any resources, and (2) the extent of this overlap.

As we will discuss below, there are some analogies between language and visual recursion, in what concerns the abstraction of the representations and the processing advantages that they afford, for example in parsing fine information embedded within hierarchical structures (Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014; Roeper, 2011). However, this capacity in different domains might be instantiated by completely segregated cognitive and neural resources. Instead, these analogies might result from general principles of computational efficiency. Therefore, it remains an open empirical question (which we will not address here) whether there is a supra-modal "recursion network", or whether each domain supports its own domain-specific 'recursion module' (see Tettamanti and Weniger (2006) for a similar discussion).

In this manuscript, we aim at investigating the neural mechanisms involved in the representation of visuo-spatial hierarchies using recursive principles, in comparison with the representation of the same hierarchies using non-recursive rules. In particular, we want to investigate whether the representation of visual recursion specifically correlates with the Default Mode Network (DMN), a brain system known to be involved in the processing of internal information.

In the current literature investigating recursion empirically, in language and other domains, a particular pair of prerequisites seems to be assumed (Fitch, 2010; Hornstein & Nunes, 2008; Martins, 2012; Zaccarella, Meyer, Makuuchi, & Friederici, 2015). The first is the existence of a computational process able to combine elements and form a new dominant supra-ordinate element, for example, the combination of [student]$_{NP}$ and [committee]$_{NP}$ to form [[student]$_{NP}$ committee]$_{NP}$. The second prerequisite is the particular kind of labels, categories or roles, that are attributed to both the dominant and subordinate elements (in this example, both simple and compound nouns are labeled as Noun Phrases or NP). If both dominant and subordinate elements are represented as having similar categories or labels (Fig. 3B), then they share affordances regarding how they can be further combined to form new supra-ordinate elements. These shared combinatorial affordances, provided when the same particular categories are used to represent elements in different hierarchical levels, are the key to hierarchical self-similarity and to (potential) infinite hierarchical depth.

While some groups have been focusing on the kind of combinatorial processes involved in building recursive hierarchies (Friederici, 2011; Petersson & Hagoort, 2012; for reviews), here we focus on the ability to attribute similar labels to elements belonging to different hierarchical levels. This approach is implied in many theoretical accounts of language processing (e.g., Cognitive Grammar (Landauer et al., 1997), Construction Grammar (Croft, 2001), or Parallel Architecture (Jackendoff, 2002)) in which words and syntactic rules are understood as different variants of schemas, in that they are "pieces of stored structure" in the long-term memory (Jackendoff, 2015). What makes a schema rule-like is that some of its structure consists of variables of a certain category, "such as V [verb] and NP [noun phrase] in a VP [verb phrase] schema" (Jackendoff, 2015). This approach, being grounded in conceptual semantics (Jackendoff, 1983), can be easily extended to several domains of cognition, such as spatial and social cognition (Jackendoff, 1987, 2007; Landau & Jackendoff, 1993), and provides an interesting perspective on the interface between the conceptual structures of different domains. For instance, Pulvermüller and Fadiga (2010) have analyzed how sensory-motor and linguistic schemas might share some of their underlying structure, both in semantics and grammar. Crucially, such conceptual structures are probably stored in the semantic conceptual system, which processes not only "semantics" in a linguistic sense, but constitutes a broader repository of categories and schemas, including concrete concepts such as "dog" (Pulvermüller & Fadiga, 2010) but also more abstract ones, such as animal NP, linguistic thematic roles (Zaccarella et al., 2015), or even schematic rules such as [[NP] NP]. This focus on the conceptual and semantic system as the potential locus of shared
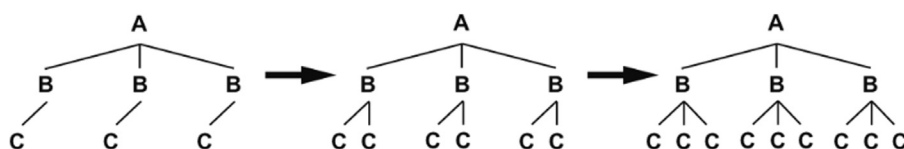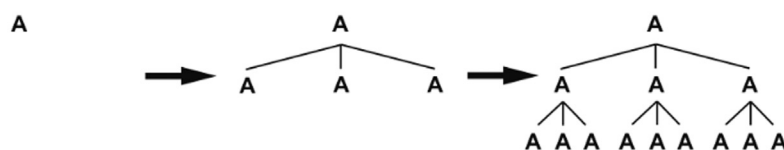
Fig. 3 — Distinction between generation rules: (A) Non-recursive processes generating hierarchies — which simply add elements to pre-existing levels — and (B) recursive hierarchies — which generate new levels (adapted from Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014).

resources between language and the visuo-spatial domains is supported by the recent discovery of hexagon grid-like neural patterns encoding both conceptual and spatial information within the DMN (Constantinescu et al., 2016). Again, these similarities might be caused by either supra-modal resources or by common principles of computational efficiency. In this manuscript, we will focus on the empirical relationship between visuo-spatial recursion and the DMN.

In sum, understood as the capability to process hierarchical self-similarity, recursion allows the generation of multiple hierarchical levels by using simple combinatorial rules and self-similarity schemas (Fig. 3). Because structures with similarities across hierarchical levels occur in many cognitive domains (see above) the cognitive ability to represent hierarchical structures as generated recursively may increase the efficiency of hierarchical processing. Even if different combinatorial processes and neural mechanisms underlie the instantiation of recursion in different domains (with the pathways of language processes being particular well-known (see Berwick, Friederici, Chomsky, & Bolhuis, 2013; Catani, Jones, & Ffytche, 2005; Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006 for reviews), these processes would still require the generation and recruitment of abstract categories and schemas that represent the similar combinatorial affordances of elements across hierarchical levels. In accordance with this idea, hierarchical processing in different domains seems to require access to areas within the temporal cortex which are involved in semantic and categorical processing. This is true for language (Ding, Melloni, Zhang, Tian, & Poeppel, 2016; Pallier, Devauchelle, & Dehaene, 2011; Zaccarella et al., 2015), music (Koelsch & Siebel, 2005; Koelsch, 2006), complex arithmetic operations (Andres, Michaux, & Pesenti, 2012; Delazer et al., 2003; Friedrich & Friederici, 2009), visual-spatial processing (Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014), and applies to more abstract auditory patterns, both in humans and non-human primates (Wang, Uhrig, Jarraya, & Dehaene, 2015).

The current study is based on the observation that hierarchical structures can be generated using different rules or principles. Of particular interest is the distinction between recursive rules − defined by a single rule characterizing several hierarchical levels − and non-recursive iterative principles − in which each hierarchical level is characterized by its own idiosyncratic rules, different from those for the other levels (Martins, 2012, Fig. 3). Since recursion allows the representation of multiple levels by a single rule, this reduces the amount of information necessary to represent hierarchies, in comparison with iterative representations of similar structures. This theoretical advantage of recursion (Koike & Yoshihara, 1993; Martins, 2012) predicts that representing hierarchies as non-recursively generated should be more cognitively demanding and thus less efficient. Recent empirical work confirmed this theoretical prediction; for instance, in the processing of visuo-spatial hierarchies, non-recursive representations were found to recruit specific visuo-spatial working memory resources to a greater extent than did recursive representations (Martins, Fischmeister, et al., 2014; Martins, Martins, & Fitch, 2015). Interestingly, although the ability to represent visual structure as recursive is harder to

acquire, once available, it appears to facilitate some aspects of hierarchical processing (Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014). Crucially, this also suggests that different cognitive systems may be used to represent similar hierarchical structures, and that recursive representations may depend more on rules operating over abstract categories that first need to be acquired and internalized (in long-term memory) before they can be successfully used. In contrast, the representation of hierarchies using non-recursive iterative principles seems to depend more on general visuo-spatial processing abilities, and less on internal representations.

Given that using internalized recursive rules based on abstract categories may reduce the information load necessary to represent hierarchical structures, we hypothesized that the DMN would be of particular importance to instantiate these rules. The DMN, a 'task-negative' network, is typically associated with self-referential or internally focused information processing (Raichle et al., 2001). The core areas of the DMN are anti-correlated with the activation of the Fronto-Parietal Control Network (FPCN), a 'task-positive' network which supports cognitive control and allocation of resources to externalized information processing (Fox et al., 2005; Power & Petersen, 2013; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). The DMN has also been shown to be closely related with categorical processing as well as the retrieval of abstract categories (Binder, Desai, Graves, & Conant, 2009; Humphreys, Hoffman, Visser, Binney, & Lambon Ralph, 2015). Furthermore, the DMN has been shown to contain gridlike structured patterns representing conceptual and spatial information (Constantinescu et al., 2016). However, this relationship might be specific to certain specific areas within the DMN (e.g., anterior temporal lobe) and dependent on the kind of stimuli used (Humphreys et al., 2015). Because recursively generated hierarchies require access to more abstract categories (Fig. 3) which synthesize the features of several hierarchical relations in a single rule, we hypothesized that this might be achieved via formation and retrieval of schemas that operate over abstract elements (Jackendoff, 2003). Again, the usage of such internalized information would reduce the reliance on domain-specific bottom-up cognitive resources. These theoretical predictions are consistent with previously published behavioral data showing that recursion in vision is less correlated with visuo-spatial memory and more correlated with domain-general hierarchical capacities (Tower of Hanoi task) (Martins, Fischmeister, et al., 2014; Martins et al., 2015).

A recent neuroimaging study also suggested that, in the representation of recursion, the DMN−FPCN balance may indeed be specifically biased towards DMN. Martins, Fischmeister, et al. (2014) investigated brain activation differences between recursive and iterative (non-recursive) hierarchical representations during processing of self-similar visual structures. They found that the representation of recursive generating principles differed from non-recursive representations in various brain areas commonly associated with the integration of spatial and categorical information and semantic processing. Although not discussed by the authors, the same brain areas can be seen as part of the DMN and the FPCN when seen from the perspective of resting-state activity. These components of the DMN are thus more active during

recursive cognition and the FPCN is more engaged with non-recursive cognition.

Given this previous observation, we aimed here to extend this previous analysis by adding resting-state measurements and additional data analyses to investigate this partial segregation of recursive and non-recursive representation rules in the visual domain at the functional network level. To our knowledge, this is one of the first attempts to demonstrate that the DMN and FPCN can be used to characterize different cognitive tasks regarding their requirements for processing 'external' (bottom-up) and 'internal' (top-down) information. The goal was to investigate which of these networks support specific aspects of hierarchical cognition. Since the understanding of recursion allows the processing of hierarchical structures via reference to a single internalized rule (abstract visual schema) and is thus less stimulus-driven, we hypothesize that the DMN may be specifically important for the processing of hierarchies when these are represented as containing cross-level similarity, i.e., when these are represented as recursive. Because of the interesting cross-domain analogies reviewed above, we hope that this study will stimulate replications in different domains. However, it is important to stress that the research presented here pertains only to the representation of visuo-spatial structures and its relationship with the DMN.

## 2. Materials and methods

2.1. Participants

Thirty-five healthy participants (19 males and 16 females, age range 20–32) were included in this study. Participants were recruited online, were right-handed native German speakers, mostly university students, and had no history of medical, neurological or psychiatric disease. Participants were paid 30 Euros for their participation. Note that these participants constitute a subgroup of those used in a recent distinct analysis (Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014); five participants from the original study were excluded since for various reasons no resting-state task data were collected. All subjects gave informed written consent prior to participation in the study, which was approved by the appropriate ethics committee of the Medical University of Vienna.

2.2. Hierarchical structures task

The task used in this functional Magnetic Resonance Imaging (fMRI) experiment has been described in detail elsewhere (cf. Martins & Fitch, 2015; Martins, Laaha, et al., 2014) and consisted of fMRI compatible adaptations of the Visual Recursion Task (VRT) and Embedded Iteration Task (EIT) (Martins, 2012).

Both tasks are forced-choice procedures using identical target stimuli (see Fig. 4A and B iteration four). In the Visual Recursion Task (VRT, cf. Fig. 4A), self-similar hierarchical structures are generated via a recursive procedure, with each step of the procedure explicitly shown in a sequence of images. Generation of this sequence is based on simple generative recursive embedding rules, like "Add three As underneath each A" as shown in Fig. 3B, which are applied to plain geometric shapes. For each rule-shape combination four iterations were generated plus one foil structure corresponding to an "incorrect" fourth iteration. In the non-recursive EIT the same end targets are generated, but via the iterative embedding of elements within a fixed hierarchical level, again
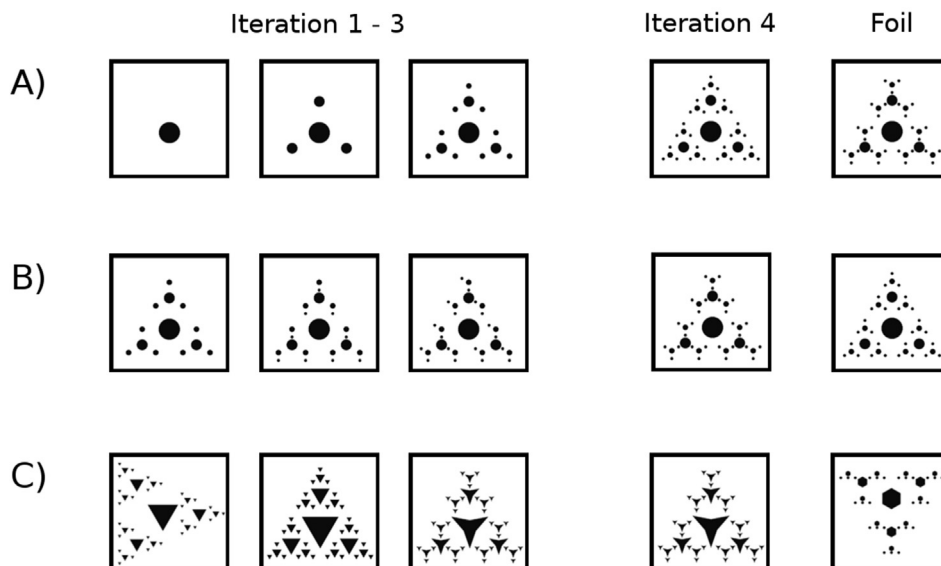
Fig. 4 – Representative examples of used items: Left the first three iterations, used for the rule acquisition phase are shown, right the correct fourth iteration and a possible foil structure used for the application phase, are presented. (A) Visual Recursion Task, (B) Embedded Iteration Task and (C) Positional Similarity Visual items used for the control task. Note that the target stimuli, i.e., the correct fourth iteration, are identical and only the generating rule recursive (A) or non-recursive (B) differentiate between the two tasks.

explicitly displayed as a sequence of images. An example for such an iterative embedding can be found in Fig. 3A and implemented in Fig. 4B. Again four iterations using iterative embedding rules were generated plus one foil structure. Foil structures for both tasks were created using different generation principles to prevent participants from applying simple heuristic comparison strategies.

Memory demands were balanced across tasks by requiring only a single rule (one recursive rule or one non-recursive rule) to progress from image to image in the sequence (see Figs. 3 and 4A and B). In addition, a positional similarity problem was introduced as a control task, which requires a simple comparison of hierarchical structures without any rule-based reasoning. This control task was introduced to account for basic visual processing effects, and any non-rule based cognitive effort (Fig. 4C). This setup allows a direct comparison of recursive cognition with non-recursive cognition while processing hierarchies. Crucially, these comparisons are not biased by simple perceptual strategies based on visual complexity, entropy or spatial frequencies since these are implausible to explain VRT performance (Martins et al., 2015).

Each trial consisted of two phases. First, in the rule acquisition phase, the first three iterations generating a visual hierarchy, or three randomly selected hierarchical images in the control task, were presented for a fixed duration of 3 sec. This phase was followed by a rule application phase in which two additional images were simultaneously presented in the bottom half of the screen, one corresponding to the correct fourth iteration and the other to a foil stimulus which failed to continue the process shown in the previous image sequence (see Fig. 5). These images were displayed for a maximum of 6 sec or until subjects responded. Participants were asked to

choose the image they that correctly continued the sequence (according to the iterative or recursive rule). In the control task, the correct image was identical to one of the three previously presented images. Before the rule acquisition phase, a single letter indicated the forthcoming task category (recursive, non-recursive or control task). The subsequent rule acquisition and rule application phases were separated by a cross-hair that was presented for a variable duration between 1000 and 3000 msec. Prior to the experiment, participants practiced with one or two blocks of the experimental tasks (with different stimuli than in the MR). The functional data acquisition consisted of four sessions, with each session consisting of 14 recursive stimuli, 14 iterative stimuli, and eight similarity (control) items. In order to prevent possible sequence effects showing learning or carry-over effects, sessions were presented in random order.

To familiarize everyone with the experiment and the tasks participants were invited to a first experimental session one week before the fMRI acquisition. Following instruction about the generation of hierarchies and the rules involved in VRT and EIT, participants performed a training session using different stimuli than those applied later inside the scanner.

2.3. Resting state

For the task-free resting-state acquisitions, participants were presented with a black screen for about 7 min and instructed to relax with eyes opened, lay still but not fall asleep and to not think of anything in particular (Kollndorfer, Fischmeister, Kasprian, Prayer, & Schöpf, 2013). Both monitoring during the acquisition and post experimental interviews confirmed that subjects stayed awake with open eyes throughout the whole
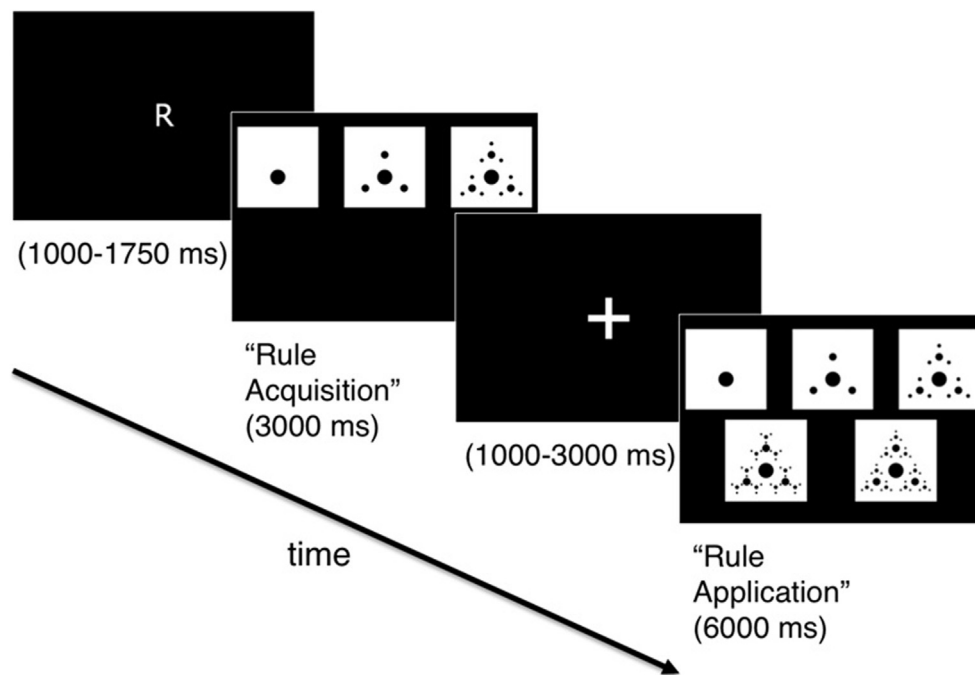
Fig. 5 — The experimental paradigm: Each trial started with a letter indicating the stimulus category followed by the rule acquisition phase, presenting the first three iterations for 3 sec. This phase was followed by a rule application phase presenting the correct fourth iteration or a foil stimulus. Here a recursive task is shown. See text for further details (adapted from Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014).

session. Measurement of the resting-state condition was conducted between session two and three of the cognitive tasks for all subjects. This way, differences in attentional levels throughout the resting-state were controlled for.

2.4. Image acquisition and preprocessing

Data acquisition was performed on a 3-Tesla TIM Trio system (Siemens, Erlangen, Germany) using a 32 channel Siemens head coil. Functional magnetic resonance images (fMRI) were acquired using an optimized 2D single-shot echo planar imaging (EPI) sequence involving EPI distortion correction via PSF mapping (Zaitsev, Hennig, & Speck, 2004). 350 EPI volumes per session were acquired with a square FOV of 220 mm, an in-plane matrix size of 128 × 128, with 36 slices aligned parallel to the AC-PC plane with 2.7 mm thickness (i.e., 2.3 mm × 2.3 mm × 2.7 mm voxel size) and 20% gap, a repetition time (TR) of 2000 msec, echo time (TE) 32 msec, and a flip angle of 73°. In addition 200 EPI volumes corresponding to 6 min 40 sec of resting-state were acquired using the same parameters as for the task-based images. For anatomical registration, high-resolution T1-weighted MR images were acquired using a 3D MPRAGE sequence (TE = 3.02 msec, TR = 2190 msec, inversion time [TI] = 1300 msec) with a matrix size of 250 × 250 × 256, with isometric voxels with a nominal side length of .9 mm, flip angle of 9° and GRAPPA acceleration factor 2.

All acquired data were analyzed using SPM 8 (http://www.fil.ion.ucl.ac.uk/spm/), the CONN functional connectivity toolbox version 14.i (Whitfield-Gabrieli & Nieto-Castanon, 2012) and in-house developed MATLAB (The Mathworks, Natick, MA, USA) scripts. Image preprocessing involved slice time correction to the middle slice and realignment to account for motion. Corrected data were then spatially normalized using New Segment (SPM manual, FIL Group) and finally smoothed using an 8 mm full-width-at-half-maximum Gaussian filter (Fischmeister et al., 2013).

2.5. Functional connectivity analysis

Seed based functional connectivity analysis has been shown to require additional preprocessing steps to prune the single voxel BOLD signal time-series from temporal confounds like residual subject motion and physiological artifacts (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012; Van Dijk et al., 2010). These temporal confounding signals were calculated from the motion realignment parameters and their Volterra expansions, session specific block regressors, and temporal BOLD signals with their derivatives calculated from white matter and CSF areas using the aCompCor method (Behzadi, Restom, Liau, & Liu, 2007). Residual BOLD time-series were then obtained by regressing each of the temporal confounds from the single voxel BOLD signal, performed separately for task data and resting-state data.

To avoid local task activation related biases in connectivity estimates, due to cross-task activations or across-trial mean changes, task-related data were additionally preprocessed using a task regression step similar to Fair et al. (2007). This way, task specific functional connectivity

estimates are not confounded by e.g., simple task-driven co-activations between neuronal areas, and thus are not purely driven by a common main task effect. Data for this regression step were obtained from a separate functional activation analysis similar to Martins, Fischmeister, et al. (2014) and Martins, Laaha, et al. (2014) and then added as confound − again using aCompCor (Behzadi et al., 2007). Unlike in Martins, Fischmeister, et al. (2014) and Martins, Laaha, et al. (2014), the complete time period comprising the rule acquisition and the rule application phases was modelled as a whole for this study. This time window (about 9 sec due to the variable nature of subjects' responses) represents the critical cognitive modes (recursive or non-recursive cognition) and is sufficient to generate representative connectivity data. Since subjects' differences in response time are reflected in the model, differences in reaction time are accounted for.

Contrary to standard resting-state analysis only a high-pass filter (<.001 Hz excluded) but no low-pass temporal filter was applied since a low-pass filter would have also removed possible task-related higher frequency signals.

These data were then used to estimate resting state networks (RSNs) and task-based networks using a seed-to-voxel approach. Definition of seed regions was based on recent publications defining a representative parcellation of the human brain: resting-state functional connectivity parcellation (Cohen et al., 2008) and task meta-analysis (Power et al., 2011). This parcellation results in 264 representative brain regions which can be pooled into several highly correlated communities. In a recent consensus analysis these communities could be assigned to well-known brain networks, like task-relevant control networks, e.g., the FPCN, or the DMN (Cole et al., 2013; Power & Petersen, 2013). These assignments were used to generate two summary subsets, one representing the DMN as task negative and the other representing the FPCN as a task positive network (see Table 1 for details of the selected locations). For each of these DMN/FPCN summary sets an average signal time course was extracted for each task and the resting state condition. These average signal time courses represented the 8 seed time courses used as input for a seed-to-voxel functional connectivity analysis: DMN-Rest input, FPCN-Rest input, DMN-Recursive input, FPCN-Recursive input, DMN-Non-Recursive input, FPCN-Non-Recursive input, DMN-Control input, FPCN-Control input. These 8 inputs were used for a Pearson correlation between the seed time courses and all brain voxels. The resulting DMN related and FPCN related networks were finally converted using Fisher's Z-transformation for second-level analysis. This procedure defines eight different networks per subject: (1) DMN-Rest network: brain areas the time courses of which are significantly correlated with the DMN-Rest input during the resting state condition, (2) DMN-Recursive network: brain areas correlating with the DMN-Recursive input during the recursive condition, (3) DMN-Non-Recursive network: brain areas correlating with the DMN-Non-Recursive input during the non-recursive condition, (4) DMN-Control network: brain areas correlating with the DMN-Control input during the control condition and (5)−(8) the corresponding FPCN networks, respectively. For every network the subject-specific

Table 1 – Definition of DMN and FPCN seeds. Selected subsets of the 264 brain regions analysis (Power et al., 2011) used for the definition of the Default Mode Network (DMN) and the Fronto-Parietal Control Network (FPCN). Anatomical labels are based on probabilistic maps.

Network system	Brain region	MNI x	y	z
Default Mode Network	Parietal Cortex			
	Left angular gyrus	−44	−65	35
	Left Angular Gyrus	−39	−75	44
	Left Middle Cingulate Cortex	−2	−37	44
	Left Precuneus	−13	−40	1
		−7	−55	27
		−11	−56	16
		−3	−49	13
	Right Angular Gyrus	52	−59	36
		47	−50	29
	Right Posterior Cingulate Cortex	8	−48	31
	Right Precuneus	6	−59	35
		15	−63	26
		11	−54	17
	Temporal Cortex			
	Left Fusiform Gyrus	−34	−38	−16
	Left Medial Temporal Pole	−44	12	−34
	Left Parahippocampal Gyrus	−26	−40	−8
	Left Middle Temporal Gyrus	−46	−61	21
		−68	−23	−16
		−56	−13	−10
		−58	−30	−4
		−68	−41	−5
		−53	3	−27
		−49	−42	1
	Right Fusiform Gyrus	27	−37	−13
	Right Middle Temporal Gyrus	65	−12	−19
		65	−31	−9
		52	−2	−16
		52	7	−30
	Frontal Cortex			
	Left Anterior Cingulate Cortex	−7	51	−1
	Left Anterior Cingulate Cortex	−11	45	8
		−3	42	16
	Left Inferior Frontal Gyrus p. Orbitalis	−46	31	−13
	Left Mid Orbital Gyrus	−3	44	−9
	Left Middle Frontal Gyrus	−35	20	51
	Left Superior Frontal Gyrus	−16	29	53
		−10	55	39
		−20	45	39
		−20	64	19
	Left Superior Medial Gyrus	−10	39	52
		−2	38	36
		−8	48	23
	Left Superior Orbital Gyrus	−18	63	−9
	Right Anterior Cingulate Cortex	12	36	20
	Right Inferior Frontal Gyrus p. Orbitalis	49	35	−12
	Right Medial Temporal Pole	46	16	−30
	Right Mid Orbital Gyrus	6	67	−4
		8	42	−5
	Right Rectal Gyrus	8	48	−15
	Right Superior Frontal Gyrus	23	33	48
		22	39	39

Table 1 – (continued)

Network system	Brain region	MNI x	y	z
	Right Superior Medial Gyrus	13	55	38
		6	54	16
		6	64	22
		9	54	3
		13	30	59
	Occipital Cortex			
	Left Middle Occipital Gyrus	−41	−75	26
	Right Middle Occipital Gyrus	43	−72	28
Fronto-Parietal Control Network	Parietal Cortex			
	Left Angular Gyrus	−42	−55	45
	Left Inferior Parietal Lobule	−53	−49	43
		−28	−58	48
	Right Inferior Parietal Lobule	44	−53	47
	Temporal Cortex			
	Right Inferior Temporal Gyrus	58	−53	−14
	Right SupraMarginal Gyrus	49	−42	45
	Frontal Cortex			
	Left Inferior Frontal Gyrus	−47	11	23
		−42	25	30
	Left Middle Frontal Gyrus	−42	38	21
		−34	55	4
		−42	45	−2
	Left Precentral Gyrus	−44	2	46
		−41	6	33
	Left Superior Frontal Gyrus	−23	11	64
		−3	26	44
	Right Angular Gyrus	37	−65	40
		33	−53	44
	Right Inferior Frontal Gyrus	47	10	33
		48	25	27
	Right Middle Frontal Gyrus	38	43	15
		32	14	56
		40	18	40
	Right Middle Orbital Gyrus	34	54	−13
		43	49	−2
	Right Superior Orbital Gyrus	24	45	−15

connectivity estimates were entered into a repeated measures GLM with partitioned error variances for second-level analysis. This one-way rm-GLM (with each condition representing one level) allows us to answer distinct connectivity-related questions within a single statistical model. For example differences between recursive and non-recursive cognition corresponding to our primary hypothesis, can be extracted and evaluated by directly contrasting these two processes, without the need to factor out non-rule-based reasoning (the control task). This is possible since all non-rule-based processes are implicitly subtracted from all hierarchical conditions by including the control-task in the overall model. Additionally, one-sample *t*-tests were calculated to show resting and task-related positive and negative functional connectivity within DMN and FPCN related areas. All task-based comparisons were masked with the respective resting-state connectivity maps. To this end individual DMN-Rest and FPCN-Rest networks were submitted to single-subject *t*-test, resulting interconnected brain areas were

thresholded and binarized and subsequently used as neuroanatomical masks to restrict the analysis of task-related networks to these specific rest networks. This allows us to constrain obtained results from single comparisons to one single rest network without biasing results as a direct comparison or an a-priori masking would have done. All resulting statistical connectivity maps were thresholded at voxel-wise $p < .001$ and a cluster extent of $p < .05$, FDR.

3. Results

3.1. Behavioral

During fMRI data collection all participants performed well and no-one reported any difficulties with the item material or the tasks. All participants showed high rates of correct responses across all three tasks. On average participants score 95.5% correct in VRT ($SD = 5$), 91.4% correct in EIT ($SD = 7$) and 96.1% correct in PSVT ($SD = 6$). Nevertheless, there was a significant difference in task performance between the three (repeated-measures ANOVA: $F_{2,68} = 15.322$, $p < .001$, Greenhouse-Geisser corrected) with participants scoring significantly lower in EIT than in VRT ($df = 34$, $t = -4.75$, $p < .001$) and PSVT ($df = 34$, $t = -3.99$, $p < .001$). Mean reaction time for all tasks were comparable, yet there was a significant difference in response time (repeated-measures ANOVA: $F_{2,68} = 5.961$, $p = .01$, Greenhouse-Geisser corrected). Unlike in performance, VRT showed the lowest response time ($rt = 2.34$ sec, $SD = .57$) and was significantly different from EIT ($rt = 2.56$ sec, $SD = .66$; $df = 34$, $t = 4.691$, $p < .001$) and from PSVT ($rt = 2.55$ sec, $SD = .52$; $df = 34$, $t = 2.80$, $p < .008$). These differences in task-performance and response time were not found during the pretesting which was conducted one week before the MR session to familiarize everyone with the tasks and conditions. Thus, observed minimal differences can

likely be explained by the novel and challenging environment while inside the scanner.

3.2. Resting state functional connectivity

For the DMN-Rest condition, DMN-related cortical regions within the medial frontal cortex and the medial and inferior lateral parietal cortex and the temporal cortex were delineated as significantly connected. Within these, the medial frontal cortex activation formed the largest connectivity cluster, ranging from the mid orbital gyrus through medial frontal regions to the superior medial gyrus. The two parietal connectivity clusters cover medial and posterior cingulate cortex and the precuneus, and the left and right angular gyrus within the inferior parietal lobe. Other regions such as the hippocampal formation previously associated with the DMN were also significantly connected within our DMN-Rest network (cf. Fig. 6A, Table 2). Overall the DMN-Rest network comprised all DMN core areas as previously defined (ventral and dorsal medial prefrontal cortex, posterior cingulate/retrosplenial cortex, inferior parietal lobule, lateral temporal cortex, and hippocampal formation; see Buckner, Andrews-Hanna, & Schacter, 2008).

Correspondingly, the functional connectivity pattern for the FPCN comprised the FPCN core areas as previously defined (Cole & Schneider, 2007; Vincent et al., 2008). Our connectivity clusters included the middle frontal cortex extending laterally toward the opercular and triangular part of the inferior frontal gyrus, the medial superior frontal gyrus and the anterior inferior parietal lobe of both hemispheres. Next to these representative FPCN areas other brain areas within the temporal cortex were also found to be significantly correlated with this canonical FPCN-Rest network (see Fig. 6B, Table 2 for a detailed listing).

For analysis of the task-based functional connectivity results, described in the next section, the significantly connected areas of the DMN-Rest and FPCN-Rest networks were
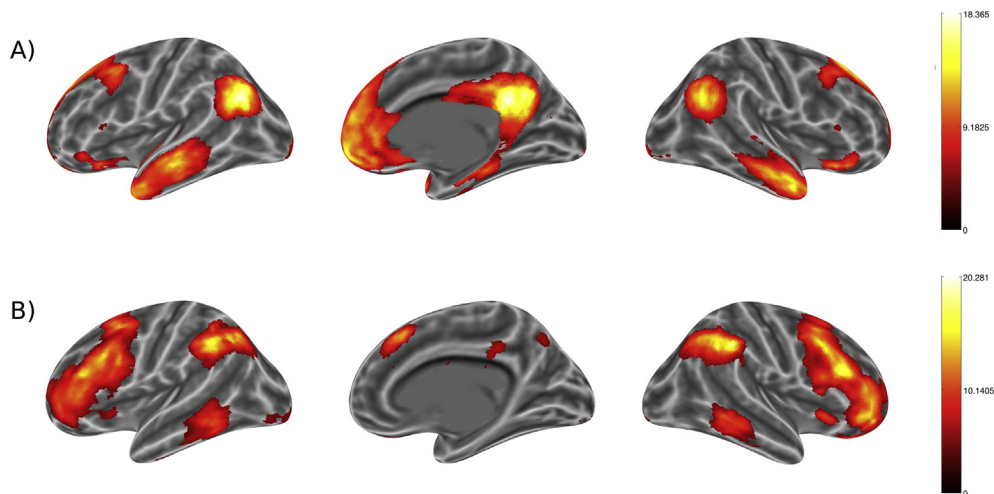
Fig. 6 − Resting-state architecture of the Default-Mode Network (A) and the Frontal-Parietal Control Network (B) in our subject population. Seed regions for this functional connectivity analysis delineating the DMN and the FPCN were based on a functional connectivity parcellations of the brain, cf. Cohen et al. (2008) and Power et al. (2011) and Table 1. Resulting network activations, MNI coordinate and anatomical labels are given in Table 2.

Table 2 – Resting state networks. Note that anatomical labelling is based on probabilistic maps using MNI coordinates. All presented regions exceed a combined voxel-wise threshold of $p < .001$ and a cluster extent of $p < .05$, FDR.

Brain region	MNI			T-value
	x	y	z	
Default-Mode Network **Medial Frontal Cluster**				
Right Mid Orbital Gyrus – right Area Fp1	4	68	−2	15.87
Left Superior Medial Gyrus – left Area Fp2	−2	56	10	15.42
Left Mid Orbital Gyrus – left Area Fp2	−8	58	−10	15.37
Left ACC	−2	50	6	14.86
Left Mid Orbital Gyrus – left Area Fp2	−6	48	−8	14.69
Right Superior Medial Gyrus	8	52	20	13.4
Mid Parietal Cluster				
Right PCC	6	−48	26	18.1
Right Precuneus	4	−56	28	17.55
Left Precuneus	−8	−58	34	16.89
Left MCC	−8	−44	34	15.66
Left and right Lateral Parietal Cluster				
Left Angular Gyrus – left Area PGp – Inferior Parietal Lobe	−42	−62	30	18.36
right Angular Gyrus – right Area PGp – Inferior Parietal Lobe	54	−60	28	15.92
Left and right Temporal Cluster				
Left Middle Temporal Gyrus	−52	−24	−10	14.48
Left Inferioright Temporal Gyrus	−40	10	−34	11.84
Left Medial Temporal Pole	−44	12	−32	11.26
Right Middle Temporal Gyrus	56	2	−30	15.89
Right Medial Temporal Pole	44	6	−32	12.37
Hippocampal Cluster				
Right ParaHippocampal Gyrus – right Subiculum	26	−34	−12	9.96
Right ParaHippocampal Gyrus – right Hippocampus)	24	−16	−22	9.26
Occipital Cluster				
Left Middle Occipital Gyrus – left hOc2 [V2]	−20	−102	−6	6.75
Left Calcarine Gyrus – left hOC1 [V1]	−10	−104	−4	6.6
Right Linual Gyrus – right hOC1 [V1]	20	−100	−10	8.15
Right Inferioright Occipital Gyrus – right hOc4v [V4(v)]	46	−86	−12	5.75
Right Superioright Occipital Gyrus – right hOc2 [V2]	22	−100	12	5.31
Right Middle Occipital Gyrus – right hOc2 [V2]	28	−100	8	5.06
Fronto-Parietal Control Network **Right and Left Prefrontal Cluster**				
Right Inferior Frontal Gyrus p. Triangularis	46	28	26	17.76
Right Middle Frontal Gyrus	42	16	40	17.25
Right Middle Orbital Gyrus	36	54	−14	15.35
Right Inferior Frontal Gyrus p. Opercularis	48	18	28	15.06
Right Inferior Frontal Gyrus p. Orbitalis	44	44	−10	14.03
Left Inferior Frontal Gyrus p. Triangularis	−44	34	20	16.74
Left Inferior Frontal Gyrus p. Opercularis	−44	20	32	15.95
Left Middle Frontal Gyrus	−28	12	52	14.35
Left Middle Orbital Gyrus	−40	52	−10	9.77
Right and Left Inferior Parietal Cluster				
Left Inferior Parietal Lobule – left Area hIP1 (IPS)	−38	−56	46	20.28
Left Inferior Parietal Lobule – left Area hIP2 (IPS)	−46	−46	42	17.87
Right SupraMarginal Gyrus – right Area hIP1 (IPS)	50	−42	44	19.72
Right Inferior Parietal Lobule – right Area hIP1 (IPS)	38	−54	44	16.96
Medial Frontal Cluster				
Left Superior Medial Gyrus	−2	30	44	16.73
Right Superior Medial Gyrus	5	23	50	11.31
Right and Left Temporal Cluster				
Left Middle Temporal Gyrus	−66	−42	−12	12.48
Left Inferior Temporal Gyrus	−54	−58	−22	11.15
Right Middle Temporal Gyrus	66	−46	−6	11.93
Right Middle Temporal Gyrus	56	−42	−10	9.02

binarized and used as neuroanatomical masks to restrict further analysis to these specific networks.

3.3. Task-based functional connectivity

Analyzing task-related connectivity patterns (in recursive, non-recursive and similarity tasks) for the default-mode and the Frontal-Parietal Control Network revealed stable and reliable connectivity patterns. Interestingly, all three tasks showed very similar patterns of connectivity with respect to connectivity estimates within DMN and FPCN related areas (Fig. 7). DMN-related cortical regions comprised all DMN core areas like the ventral and dorsal medial prefrontal cortex, posterior cingulate/retrosplenial cortex, inferior parietal
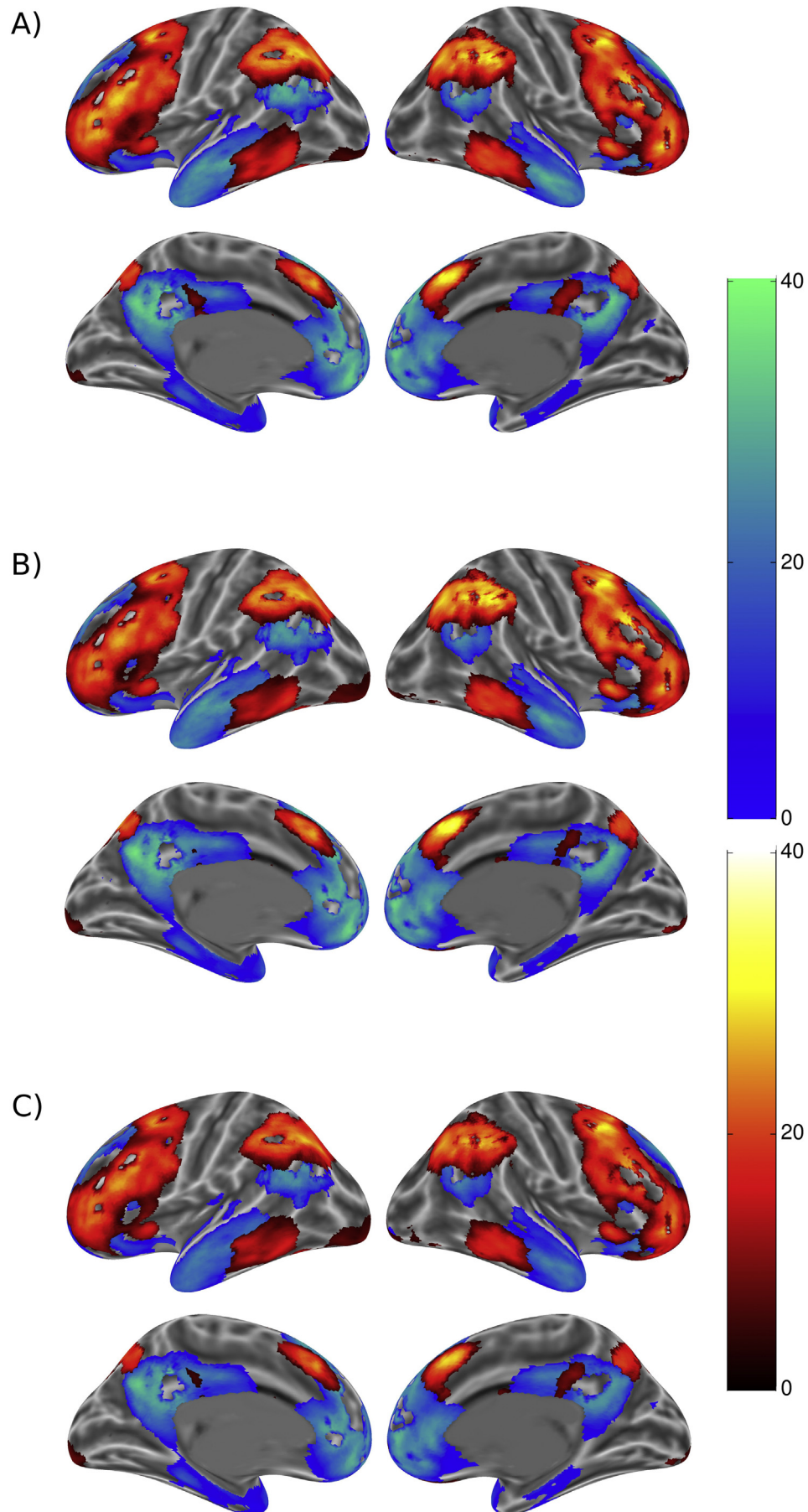
lobule, lateral temporal cortex, and hippocampal formation (Buckner et al., 2008). Task related increased connectivities within the FPCN comprised clusters along the middle frontal cortex extending laterally toward the inferior frontal gyrus, the medial superior frontal gyrus and the anterior inferior parietal lobe. Consistent with previous studies, we found decreased functional connectivity during the execution of tasks, compared to task-free periods, within DMN-related areas – in particular within anterior and parietal regions – and increased connectivity during tasks within FPCN-related areas (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Vincent et al., 2008).

A direct comparison of the representation of recursive versus non-recursive generating principles (of similar hierarchical structures) within the task-negative DMN network showed increased connectivity during the representation of recursion as compared to non-recursive representations (Fig. 8, Table 3). Note that due to the nature of the one-way rm-GLM this contrast directly compares the two rule-based processes, since any non-rule-based reasoning processes are implicitly factored out by including the control task in the model.

Such an increase in connectivity was observed in parts of the right precuneus and the DMN core areas medial prefrontal cortex, inferior parietal lobule and lateral temporal cortex (Buckner et al., 2008). Importantly, none of the DMN areas showed a significant opposite behavior, that is, no significant increases in connectivity were observed when contrasting non-recursive with recursive cognition. Furthermore, certain areas not typically associated with DMN, within the occipital cortex, showed an increased connectivity while representing recursive hierarchical rules as compared to non-recursive rule processing.

Comparing the two cognitive modes within FPCN-Rest network areas revealed the opposite behavior. Here, contrasting recursive and non-recursive generating principles yielded increased connectivity only for the representation of non-recursive hierarchical rules. Clusters with increased FPCN connectivity were found in core areas of the FPCN (compare Vincent et al., 2008) within the lateral frontal, temporal and parietal cortices (Fig. 5, Table 3). Interestingly, a non-recursive > recursive FPCN connectivity was again observed in parts of the precuneus, but in this case localized on the left side. Similar to our observations within the DMN, the opposite contrast, recursive > non-recursive processing within FPCN did not yield any significant increase.

4. Discussion

Hierarchies with some degree of self-similarity are often found in nature, identifiable by their attractive fractal structure. At a certain level of abstraction, we also find examples of

these structures in cognitive domains like language, vision, action and social processing (e.g., Corballis, 2011; Fitch et al., 2005; Hauser et al., 2002; Martins, 2012; Miller, 2009). Recent studies have shown that complex hierarchies can often be efficiently represented as generated by recursive rules (Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014), and such rules, once acquired and understood, facilitate various aspects of hierarchical processing (Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014). This led to the hypothesis that different cognitive systems can be used to represent hierarchical structures. On the one hand, the representation of recursive principles might depend on the retrieval of internalized rules and schemas that explain a large portion of incoming sensorial data, hence reducing the amount of external information necessary to maintain representations in working memory. On the other hand, the representation of hierarchies as generated non-recursively might engage fundamental bottom-up visuo-spatial processes and thus yield a more external focus, with higher reliance on domain-specific working memory (Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014; Rogers, Avery, & Heckers, 2010). These hypotheses seem to be consistent with both behavioral and neuroimaging findings (Martins, Fischmeister, et al., 2014; Martins, Laaha, et al., 2014; Martins et al., 2015).

Here we tested these hypotheses more directly, by contrasting neuronal activity during the processing of self-similar hierarchies either using recursive rules or iterative, non-recursive principles, and task-free resting-state data using functional connectivity analyses. This way we aimed to link task-evoked functional networks induced by the two cognitive processes with the resting state architecture of the DMN and the FPCN. Again, our assumption was that FPCN would signal "externally-focused" bottom-up processing, and DMN internal top-down processing, in which the representation of external information would rely less on FPCN, and more on the retrieval of internalized rules or schemas.

Functional connectivity analysis of task-related data revealed stable and reliable connectivity patterns within DMN and FPCN regions for every task. Furthermore, the well-known inverse relationship of DMN and FPCN while performing cognitive tasks was reliably found. The comparison of recursion versus non-recursive iteration revealed higher connectivity values within DMN-related brain areas for the recursive representation of self-similar hierarchies. Conversely, FPCN-related areas showed higher connectivity patterns with non-recursive representations (vs recursion) in the processing of identical images. These results suggest that representation of recursion is highly connected with DMN-related brain areas, and thus recruits more internally generated information than non-recursive representations. Non-recursive representations, on the other hand, seem to require FPCN-related areas to a higher extent, compatible with our hypothesis of a stronger domain-specific visuo-spatial processing.

Fig. 7 — **Task based connectivity results for the three tasks: Areas showing increased connectivity within Default Mode Network (shown in blue) and within the Fronto-Parietal Control Network while processing recursions (A), hierarchies (B) and non-rule based comparisions (C). Note that all three tasks showed very similar patterns of connectivity estimates within DMN-related cortical regions the Fronto-Parietal Control Network.**
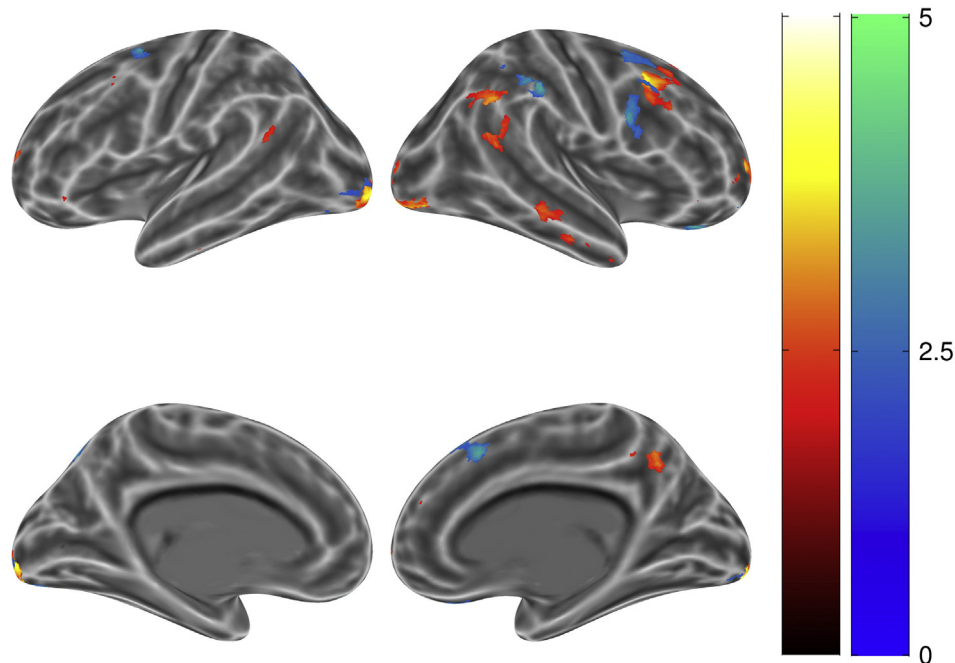
Fig. 8 – Task based functional connectivity differences: Anatomical areas with increased connectivity to the DMN inputs during recursive processing (recursive > non-recursive processing) are shown in red. In blue anatomical areas yielding increased connectivity to the FPCN inputs during non-recursive processing (non-recursive > recursive processing). Please also compare Table 2 but note that (1) only surface based activities are visible and (2) that inverse contrasts within the two networks, e.g., non-recursive > recursive processing within DMN, did not result in any significant difference.

This conclusion is compatible with the steadily increasing body of evidence suggesting that the human cortex is organized into two orthogonal and functionally distinct networks. These two networks were chosen for investigation as they represent a task-positive network — commonly associated with cognition and task processing which on the whole is externally oriented — and a task negative network (Fox et al., 2006; Raichle, 2010).

The FPCN represents an important task-positive network which plays a significant role in executive control of attention and adaptive control processes, and flexibly couples with the DMN or the dorsal attention network to support internally or externally focused goal-directed cognition (Power, Cohen, Nelson, & Wig, 2011; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010; Vincent et al., 2008). Therefore, our observation of higher connectivity within the FPCN while encoding non-recursive transformations within hierarchical structures seem to indicate a higher demand for switching between internal and external resources. Consistent with our theoretical assumptions and previous behavioral findings (Fitch & Martins, 2014; Martins, 2012) the results presented here indicate that transformations within a fixed hierarchical level indeed represent a more externally focused process compared to recursive processes.

The second network, termed the DMN (Raichle et al., 2001), is internally oriented, deals with self-related processes (Buckner et al., 2008; Vaidya & Gordon, 2013) and consists of medial cortical regions within the frontal and parietal cortex as well as of the inferior parietal lobe and temporal regions. Some of these regions have also been implicated in the

processing of semantic information (Binder et al., 2009) and abstract categories (Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). Singh and Fawcett (2008) were among the first to investigate the relation of DMN deactivation and task performance. Using a visual detection paradigm, they reported a negative correlation between task-related and DMN activations. By varying the factor 'task difficulty' and therefore implicitly modulating external attention, they observed a linear graded deactivation within DMN areas: the more external attention required (lower motion coherence of the presented stimuli) the more DMN was deactivated. This relationship between task-evoked activation, external focus, and deactivation within the DMN has since then been shown repeatedly (for a recent review see Anticevic et al., 2012) and fits well to our data. However, while Singh and Fawcett (2008) varied the level of internal information processing, our study tried to trigger different cognitive processes involved in the processing of the VRT and EIT. Crucially, we maximally constrained the item material for both hierarchical tasks with respect to physical and cognitive properties so that the representation of a single rule was sufficient to perform adequately, but the nature of this rule varied between tasks (Fitch & Martins, 2014; Martins, 2012; Martins et al., 2015). Using this procedure we aimed to isolate effects involved in the different cognitive processes necessary to instantiate the representation of recursive versus non-recursive principles for generating hierarchies. Therefore, the decreased DMN-related deactivation found while processing hierarchical structures in the VRT can be attributed to the cognitive processes underlying the representation of recursive rules.

Table 3 – Functional connectivity. Comparison 'Recursive versus non-recursive representations': anatomical areas with increased connectivity to the DMN seed during recursive representations. Comparison 'Non-recursive versus recursive representations': anatomical areas with increased connectivity to the FPCN seed during non-recursive representations. Anatomical labelling is based on probabilistic maps using MNI coordinates. Note that only positive connectivity differences exceeding a combined voxel-wise threshold of $p < .001$ and a cluster extent of $p < .05$, FDR are shown to not intermix task-positive and task-negative networks.

	Brain region	MNI			T-value
		x	y	z	
Recursive versus non-recursive rule processing within DMN related areas	**Occipital Cluster**				
	Left Inferior Occipital Gyrus – left hOc3v [V3v]	−22	−98	−8	4.1
	Left Calcarine Gyrus – left hOc3v [V3v]	−16	−94	−6	3.87
	Left Middle Occipital Gyrus – left hOc3v [V3v]	−30	−94	4	3.65
	Right Linual Gyrus – right hOc3v [V3v]	18	−90	−12	5.53
	Right Inferior Occipital Gyrus – right hOc3v [V3v]	28	−86	−16	4.48
	Right Inferior Occipital Gyrus – right hOc4v [V4(v)]	38	−84	−12	3.83
	Frontal Cluster				
	Right Middle Frontal Gyrus	40	14	56	4.59
	Right Superior Medial Gyrus	18	40	56	3.56
	Right Superior Frontal Gyrus	26	38	54	3.26
	Right Superior Frontal Gyrus – right Area Fp1	30	62	2	5.81
	Right Middle Frontal Gyrus	28	52	6	4.36
	Right Superior Medial Gyrus – right Area Fp1	8	72	10	4.01
	Right Superior Frontal Gyrus – right Area Fp1	18	70	8	3.54
	Mid Parietal Cluster				
	Right Precuneus	4	−52	42	3.87
	Lateral Parietal Cluster				
	Right Inferior Parietal Lobule – right Area PFm (IPL)	58	−54	46	3.51
	Right Inferior Parietal Lobule – right Area PGa (IPL)	50	−54	40	3.37
	Left and Right Temporal Cluster				
	Left Middle Temporal Gyrus	−50	−56	16	3.13
	Right Middle Temporal Gyrus	38	−48	18	3.46
	Right Angular Gyrus	42	−46	16	3.35
Non-recursive versus recursive rule processing within FPCN related areas	**Frontal Cluster**				
	Right Superior Orbital Gyrus	20	32	−16	3.96
	Right Superior Medial Gyrus	6	20	44	3.92
	Right Precentral Gyrus	46	8	34	3.81
	Right Inferior Frontal Gyrus (p. Opercularis)	46	8	28	3.65
	Right Middle Frontal Gyrus	48	14	44	3.33
	Left Superior Orbital Gyrus	−10	52	−22	2.68
	Left Inferior Frontal Gyrus (p. Orbitalis)	−50	34	−16	2.31
	Left Superior Orbital Gyrus	−14	48	−24	2.13
	Medial Frontal Cluster				
	Left Superior Frontal Gyrus – left Area Fp1	−24	64	8	2.74
	Lateral Parietal Cluster				
	Right SupraMarginal Gyrus– right Area PFt (IPL)	52	−32	42	3.75
	Right Superior Parietal Lobule – right Area 7A (SPL)	22	−70	56	3.42
	Right SupraMarginal Gyrus – right Area 2	42	−34	40	3.37
	Right Inferior Parietal Lobule – right Area hIP2 (IPS)	48	−38	48	2.76
	Mid Parietal Cluster				
	Left Superior Parietal Lobule – left Area 7A (SPL)	−16	−72	48	3.34
	Left Superior Parietal Lobule	−16	−66	48	2.95
	Left Precuneus	−26	−68	22	2.82
	Occipital Cluster				
	Right Calcarine Gyrus – right hOC1 [V1]	20	−100	2	3.27
	Right Linual Gyrus – right hOc3v [V3v]	18	−90	−10	2.58
	Left Fusiform Gyrus – left hOc3v [V3v]	−22	−84	−8	3.12
	Left Middle Occipital Gyrus	−24	−90	0	2.58
	Left Middle Occipital Gyrus	−36	−94	−2	2.54
	Left Middle Occipital Gyrus – left hOc3v [V3v]	−30	−96	8	2.47
	Left and Right Temporal Cluster				
	Right Superior Temporal Gyrus	62	−28	2	2.11
	Right Middle Temporal Gyrus	64	−42	−2	1.95
	Right Inferior Temporal Gyrus	64	−22	−24	1.93
	Left Middle Temporal Gyrus	−66	−28	−10	2.95
	Left Inferior Temporal Gyrus	−56	−14	−32	2.37

Recently, the homogeneous nature of the DMN has been challenged, and initial evidence provided by Andrews-Hanna, Reidler, Sepulcre, Poulin, and Buckner (2010) suggested the existence of two subsystems, each subserving distinct internal mainly self-related cognitive functions: a medial temporal and a dorsal medial frontal subsystem both highly correlated with a midline core (posterior cingulate and anterior medial prefrontal cortex). Interestingly, in our study differences between recursive and non-recursive hierarchical processing were found within dorsal medial frontal and lateral temporal cortical regions linked to the dorsal medial subsystem, and within the core of the DMN comprising, among others, ventral regions of the precuneus and the angular gyrus. In particular the core region is thought to represent a functional hub for the integration and transfer of information between the two subsystems while the dorsal medial component is commonly associated with social cognition and reflection upon self and others, using stored conceptual knowledge (see Andrews-Hanna, Smallwood, and Spreng (2014) for a detailed review). Furthermore, the anterior temporal regions of the core are critically involved in conceptual processing (Patterson, Nestor, & Rogers, 2007) and in the storage of semantic and conceptual knowledge (Binder & Desai, 2011). The angular gyrus is connected to the anterior temporal cortex and other regions of the DMN and seems to function as a cross-modal integration region combining internal and conceptual information within a spatiotemporal context with perceptual sources (Seghier & Price, 2012). This supports the hypotheses put forward here that (1) the representation of recursive principles generating hierarchies requires access to an internal mode of information-processing, that (2) this access is mediated by both the core and dorsal-medial subsystems of the DMN, and that (3) the integration of these systems enacts the role of internal rules in the processing of visuo-spatial hierarchical information (Kravitz, Saleem, Baker, & Mishkin, 2011).

Using visual comparison paradigms, Rogers et al. (2010) found similar results to those as reported here. In that study, non-sequential visual stimuli were compared with sequential stimuli, both previously learned and novel. They found DMN-related areas to be strongly functionally connected to the FPCN network while processing hierarchies as opposed to simple stimulus pairs. Interestingly, the authors could not find a memory effect induced by the learning session preceding the functional data acquisition. Thus, they suggest that the DMN maintains an internal model of hierarchical sequences used as reference - irrespective of whether they are novel or learned. Based on this observation one might speculate that certain subsystems of the DMN are not just necessary to maintain and process recursive hierarchies but also represent a core component of an internal recursive processing system.

5.   Limitations

Despite these interesting findings one could argue that our results are not due to recursion *per se*, but to simple perceptual principles, simple heuristic strategies or differences in attention. While it is difficult to control for the mental processes participants used in our paradigms, and during rest, we tried to lower the occurrence of these alternative strategies by carefully instructing and training subjects before the experiment, choosing different 'foil item categories' to block any specific heuristic strategies, and finally by explicitly contrasting all tests against a pure similarity task condition. Additionally, in particular the visual recursive task has been shown to correlate with recursive planning tasks (Tower of Hanoi), and simple perceptual strategies employing visual complexity or entropy were shown not to explain VRT performance (Martins et al., 2015). Finally, to ensure unbiased hierarchical information-processing-related connectivity estimates, an additional regression step similar to Fair et al. (2007) was employed to prune for common main task-related activation and possible confounding effect.

Our conclusion that the understanding of recursive rules generating hierarchies relies on internal representations dependent on DMN regions is currently only valid for the cognitive domain applied in this study, i.e., the visual domain. However, we suspect that the decisive difference between recursive and non-recursive representations (the reliance on abstract categories and top-down internal representations) might extend to other domains for which humans are able to build recursive representations, e.g., music and spoken language (Fitch & Martins, 2014). Future research will be necessary to test the generality of this hypothesis.

6.   Conclusion

Our results indicate that hierarchical information processing via the understanding of recursive rules is supported by the DMN. Thus the internal rule-based representation mediated by the DMN helps humans to understand hierarchical structures in complex environments. This is likely caused by the reduced load on external information processing during recursive representations, due to the use of categories dependent of internalized recursive schemas. This mode of information processing is thus closer to the default mode of human cognition.

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