Research report

Individual variation in the propensity for prospective thought is associated with functional integration between visual and retrosplenial cortex

Mario Villena-Gonzalez [a,b,c,], Hao-ting Wang [a], Mladen Sormaz [a], Giovanna Mollo [a], Daniel S. Margulies [d], Elizabeth A. Jefferies [a] and Jonathan Smallwood [a]*

[a] *Department of Psychology, University of York, Heslington, York, England, UK*
[b] *Interdisciplinary Center for Neurosciences, Pontificia Universidad Catolica de Chile, Santiago, Chile*
[c] *Laboratorio de Neurociencia Cognitiva y Social, Facultad de Psicología, Universidad Diego Portales, Santiago, Chile*
[d] *Max Planck Research Group for Neuroanatomy & Connectivity, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany*

ABSTRACT

It is well recognized that the default mode network (DMN) is involved in states of imagination, although the cognitive processes that this association reflects are not well understood. The DMN includes many regions that function as cortical "hubs", including the posterior cingulate/retrosplenial cortex, anterior temporal lobe and the hippocampus. This suggests that the role of the DMN in cognition may reflect a process of cortical integration. In the current study we tested whether functional connectivity from uni-modal regions of cortex into the DMN is linked to features of imaginative thought. We found that strong intrinsic communication between visual and retrosplenial cortex was correlated with the degree of social thoughts about the future. Using an independent dataset, we show that the same region of retrosplenial cortex is functionally coupled to regions of primary visual cortex as well as core regions that make up the DMN. Finally, we compared the functional connectivity of the retrosplenial cortex, with a region of medial prefrontal cortex implicated in the integration of information from regions of the temporal lobe associated with future thought in a prior study. This analysis shows that the retrosplenial cortex is preferentially coupled to medial occipital, temporal lobe regions and the angular gyrus, areas linked to episodic memory, scene construction and navigation. In contrast, the medial prefrontal cortex shows preferential connectivity with motor cortex and lateral temporal and prefrontal regions implicated in language, motor processes and working memory. Together these findings suggest that integrating neural information from visual cortex into retrosplenial cortex may be important for imagining the future and may do so by creating a

mental scene in which prospective simulations play out. We speculate that the role of the DMN in imagination may emerge from its capacity to bind together distributed representations from across the cortex in a coherent manner.

1. Introduction

Imagination is a core aspect of human cognition. We use it to consider what may happen in the future (Smallwood et al., 2009; Wang et al., 2016), to consider places that are distant from where we are (Peer et al., 2015), and to understand the behaviour of other people (Amodio & Frith, 2006). Imagination has many adaptive features — spontaneous thoughts about the future helps set personal goals (Medea et al., 2016) and predicts recovery from states of negative affect (Engert et al., 2014; Ruby et al., 2013), although imagination can also perpetuate states of unhappiness (Killingsworth & Gilbert, 2010). Cognitive neuroscience has demonstrated that many imaginative states depend on a large-scale neural system, anchored by hubs in medial prefrontal and posterior cingulate cortex, as well as medial and lateral regions of the temporal lobe. These regions are collectively known as the default mode network [DMN (Raichle, 2015; Raichle & Snyder, 2007)] and although their role in imaginative processes is well documented (Agnati et al., 2013), it is unclear what cognitive functions this association reflects.

The involvement of the DMN in imagination may reflect a more general role that this network plays in cognition. Imaginative processes are often highly integrated states (Schlichting & Preston, 2015): Thinking about the future, for example relies on both episodic (Hassabis et al, 2007a, 2007b) and semantic memory (Irish & Piguet, 2013), as well as affective processes (MacLeod & Byrne, 1996). Consistent with this view, many of the constituent regions of the DMN have been suggested to play an integrative role in cognition. Contemporary accounts of semantic cognition, for example, suggest that anterior temporal lobe provides multi-modal representations of conceptual knowledge by integrating signals from regions in visual, sensorimotor and auditory cortices (Lambon Ralph et al., 2017). Views of episodic memory suggest that medial temporal lobe, and in particular the hippocampus, provide sparse descriptions of past events that organize neural processing in regions of the cortex that represent specific features of the memories (such as their sensory properties, for a review see (Moscovitch et al., 2016)). Recent work has formalized this integrative account of the DMN by showing that many of the regions are located at the top of a functional hierarchy that integrates information from more specialized regions of cortex, such as visual, sensori-motor or auditory cortices (Margulies et al., 2016). This integrative architecture explains why neural signals within the DMN contain echoes of information from many different neural systems (Braga et al., 2013; Braga & Leech, 2015; Leech et al., 2012). In neural architectural terms, therefore, the DMN is well suited to provide an integrative context within which imaginative states can unfold.

Our prior work has provided preliminary support for the view that the DMN's role in cognition is the integration of information. In a cross-sectional study we demonstrated that connectivity of neural signals from "hub" regions in the medial and lateral temporal lobe into the core regions of the DMN in medial prefrontal and posterior cingulate cortex correlated with patterns of spontaneous thoughts experienced in subsequent laboratory tasks (Karapanagiotidis et al., 2016; Smallwood et al., 2016). These results are consistent with the claim that the medial core of the DMN re-represents neural signals from other cortical hub regions and that this process is important in states of imagination. The current study builds on these findings by examining two aspects of this *cortical integration hypothesis*. First, are individual differences in experiential qualities of states of imagination, such as thinking about the future, associated with the connectivity of regions of cortex with reasonably circumscribed roles (such as auditory or visual cortex)? This pattern would support the view that imaginative thought requires neural signals representing more basic features of information (such as an object's or a person's features) to be bound together. Second, do these patterns of connectivity converge on regions whose connectivity suggests an involvement of the DMN? This pattern would support the hypothesis that one function the DMN serves in imagination is to integrate signals to and from more specialized areas of cortex to produce more abstract representations of the cognitive landscape (Margulies et al., 2016).

To address these questions, we recruited a cohort of participants and measured their intrinsic neural organization using resting state functional magnetic resonance imaging (fMRI). In a subsequent laboratory session these participants completed an episodic simulation task. Prior studies have shown that the DMN is active when participants are asked to specifically generate types of thoughts about the past and the future (e.g., Addis et al., 2007). We asked participants to provide reports of experiential content when they simulated different temporal periods and used this data to explore whether individual differences in these reports predicted patterns of functional connectivity from uni-modal regions specialized in audition or vision. If integration of unimodal information into the DMN underpins the capacity for imaginative thought, then patterns of functional integration from unimodal regions linked to aspects of imagination should converge on regions of the DMN.

2. Methods

2.1. Participants

A group of 165 participants (99 females; age range 18–31, mean ± SD = 20.4 ± 2.63 years old) were recruited for this study. They were right handed, native English speakers, with

normal/corrected-to-normal vision and no history of psychiatric or neurological illness. This cohort was acquired from the undergraduate and postgraduate student body at the University of York. Participants underwent MRI scanning followed by three 2-h long behavioural testing sessions where they completed a battery of computer based tasks within a week from the scanner session. Eighteen participants were excluded from further analysis because they failed to complete the behavioural testing sessions. In total 147 participants were included in the final analyses. This study was approved by the University of York Neuroimaging Centre and by the University of York Department of Psychology ethics committees. All volunteers provided informed written consent.

Independent sample. We used an independent data set to provide independent confirmation of patterns of resting state connectivity from regions identified in this study. These data were from a publicly available data set: the Nathan Kline Institute (NKI)/Rockland Enhanced Sample.

2.2.   Task

We used a modified version of the experiment described in Addis et al. (2007). Twenty-four past and twenty-four future event trials were presented randomly across the entire session. Each trial began with a construction phase (Fig. 1, left side) during which a cueing slide was presented comprising three lines: (1) task instructions ("recall past event" or "envisage future event"); (2) the timeframe for the event ("last week" or "next week"; "last year" or "next year"); (3) a cue word. This construction phase was 20 sec long but the participant could terminate it and move to the subsequent rating phase. The trial sequence is presented in the left hand panel of Fig. 1.

When the cueing slide was displayed, participants were required to recall a past event that occurred during the specified timeframe or imagine a future event that could occur within the timeframe. The event did not have to strictly involve the object named by the cue. Participants were encouraged to freely associate so that they were successful in generating an event. Events were, however, required to be temporally and contextually specific, occurring over minutes or hours, but not more than 1 day (i.e., episodic events). Examples were provided to illustrate this requirement. Future events had to be novel (i.e., not been previously experienced by the participant) and plausible given the participant's plans for the future. Further, participants were instructed to imagine "seeing" the event from the perspective of being there rather than from an observer perspective (i.e., observing the self from an external point of view). Once participants had the event in mind (i.e., an event had been retrieved or imagined), they pressed a button on the keyboard. This response time was recorded and marked the end of event construction and the beginning of the rating phase (there was no time constraint on the rating phase, each rating slide terminated when participant made a response). The average and standard deviation of the construction phase's length for each condition was 10.37 s ± 5.64 for Last year, 10.62 s ± 6.18 for Last week, 10.56 s ± 7.41 for Next week, 10.45 s ± 5.95 for Next year. During the rating phase of each event trial, participants were provided with a number keyboard and they were asked to rate the contents of their thoughts in order to have information about multiple dimensions and characteristics of their thoughts. The questions that participants rated are presented in Table 1.

2.3.   Principal components analysis

To summarize the results of the questionnaire and rating phase, we performed an initial data reduction step using exploratory factor analysis in SPSS (IBM, version 23) following
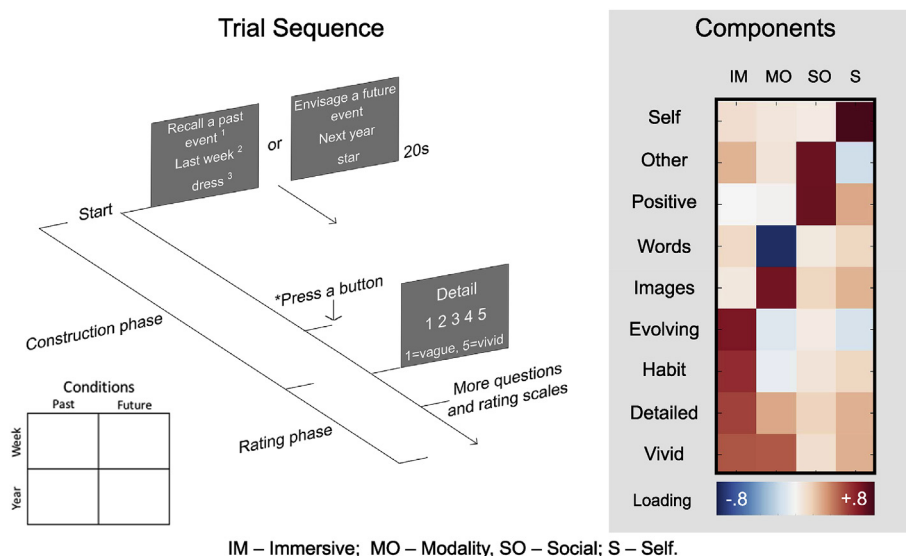

Fig. 1 — *Left hand panel.* A description of the task used to gather self-reported information on experience during the directed simulation of different temporal periods employed in this study. *Right hand panel.* Heat map describing the decomposition of the experiential descriptions generated in this experiment. The different colours reflect the loading of each question on each component, as are indicated by the colour bar.

Table 1 – **Multiple dimension experience sampling questions.**

Dimensions	Questions	0	7
Focus	My thoughts were focused on the task I was performing.	Not at all	Completely
Self	My thoughts involved myself.	Not at all	Completely
Other	My thoughts involved other people.	Not at all	Completely
Emotion	The content of my thoughts was:	Negative	Positive
Images	My thoughts were in the form of images.	Not at all	Completely
Words	My thoughts were in the form of words.	Not at all	Completely
Vivid	My thoughts were vivid as if I was there.	Not at all	Completely
Vague	My thoughts were detailed and specific.	Not at all	Completely
Habit	This thought has recurrent themes similar to those I have had before.	Not at all	Completely
Evolving	My thoughts tended to evolve in a series of steps.	Not at all	Completely

the same procedure described in Smallwood et al. (2016) and Medea et al. (2016). Questions related to temporal dimension since this was the variable we manipulated in our study. The behavioural task measures were converted into z-scores to avoid data distortions derived from the difference in score means. Missing data was imputed by mean scores. Varimax rotation was used to maximize the distinctiveness of each solution.

2.4. Resting-state fMRI recording and analyses

Structural and functional data were acquired using a 3T GE HDx Excite MRI scanner utilising an eight-channel phased array head coil (GE) tuned to 127.4 MHz, at the York Neuroimaging Centre, University of York. Structural MRI acquisition in all participants was based on a T1-weighted 3D fast spoilt gradient echo sequence (TR = 7.8 sec, TE = minimum full, flip angle = 20°, matrix size = 256 × 256, 176 slices, voxel size = 1.13 × 1.13 × 1 mm³). Resting-state activity was recorded from the whole brain using single-shot 2D gradient-echo-planar imaging (TR = 3 sec, TE = minimum full, flip angle = 90°, matrix size = 64 × 64, 60 slices, voxel size = 3 × 3 × 3 mm³, 180 volumes). Participants viewed a fixation cross with eyes open for the durations of the functional MRI resting state scan. A FLAIR scan with the same orientation as the functional scans was collected to improve co-registration between subject-specific structural and functional scans.

An independent data set was obtained from the Nathan Kline Institute (NKI)/Rockland Enhanced Sample, a publicly available data set. This allowed us to test the connectivity patterns produced in our present analyses in an independent data set. For the present purposes we used a sample containing 141 subjects that have been previously been used by Gorgolewski et al. (2014), Davey et al. (2016), and Smallwood et al. (2016). The resting state fMRI data were acquired with the following parameters: TR 2500 msec, TE 30 msec, 120 volumes, matrix size 72 × 72, 38 slices, flip angle 80°, .3 mm spacing between slices, voxel size 3 × 3 × 3 mm³ and an interleaved slice acquisition order. A high-resolution anatomical image was also acquired for each subject using the MPRAGE sequence.

Functional and structural data were pre-processed and analysed using FMRIB's Software Library (FSL version 4.1). Individual FLAIR and T1 weighted structural brain images were extracted using BET (Brain Extraction Tool). Structural images were linearly registered to the MNI-152 template using

FMRIB's Linear Image Registration Tool (FLIRT). The resting state functional data were pre-processed and analysed using the FMRI Expert Analysis Tool (FEAT). The individual subject analysis involved: motion correction using MCFLIRT; slice-timing correction using Fourier space time-series phase-shifting; spatial smoothing using a Gaussian kernel of FWHM 6 mm; grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor; high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 100 sec); Gaussian low-pass temporal filtering, with sigma = 2.8 sec.

2.5. Functional connectivity analysis

2.5.1. First level analysis
A seed-based functional connectivity analysis was carried out using seeds selected from the cortical parcellation described in Yeo et al. (2011; 17 networks). We selected the networks covering primary visual and auditory cortex. We extracted the time series from this seed and used this as explanatory variable in connectivity analyses at the single subject level. The auditory network revealed no significant results and will not be discussed further.

2.5.2. Higher level analysis
Using the FEAT fMRI toolbox, we related visual connectivity patterns to inter-individual variations in different types of thoughts using a multiple regression model, in which the connectivity map was the dependent variable and principal components of thoughts were the explanatory variables. For each of these multiple regression models, we focused on assessing the effects on temporal dimension of thought by calculating contrasts that reflected variations in this variable (e.g., principal component "future" for spontaneous thought, and "next week"/"next year" condition in the directed episodic simulation task). Within this model we characterized the unique variance that were associated with each component at each time period.

For all significant effects, we then computed the correlation between the connectivity measure for each individual and the score on the specific principal component. To control for multiple comparisons we used a cluster forming threshold of $Z = 2.6$ and controlled our Type I error rate at an alpha value of $p < .0125$ family-wise error (FWE) in order to take account of the number of voxels in the brain as well as the two tailed nature of our comparisons and the two different regression models we conducted (one for the visual seed and one for the

auditory seed). Following Eklund et al. (2016) we selected these parameters to reduce our likelihood of Type I errors. We also performed a group analysis on independent data to identify whether the overlap region resulted in previous analysis had a different functional connectivity profile to the seed regions from which the analysis was driven. All unthresholded maps were uploaded onto a publicly available collection at Neuro-vault: http://neurovault.org/collections/1854/

2.6.   Meta analytic decoding

We compared unthresholded functional connectivity activation profiles to those of previous studies using the Neurosynth decoder (Yarkoni et al., 2011). This software compared unthresholded functional connectivity activation profiles identified in the aforementioned analysis with every other meta-analytic map ($n = 11406$) for each term/concept stored in the database (e.g., semantic, episodic, spatial, memory and insight). To produce our word clouds, we manually extracted the top ten task descriptions (based on frequency) for each unthresholded z-map (we manually excluded the names of brain regions or MRI methods). This allowed us to quantify the most likely reverse inferences that would be drawn from these functional maps by the larger neuroimaging community.

3.   Results

3.1.   Decomposition of subjective reports

Visual inspection of the scree plots suggested that self-reported data obtained from the directed imagination tasks

was reasonably well described by four components (see Supplementary Fig. 1). The first component describes a dimension of immersive thought that reflects evolving and habitual experiences. The second component is anchored at one extreme by experiences taking the form of words and at the other by experiences in the forms of images. The third component reflects positive experiences that involve other people. The fourth component describes the degree of self-focus. These dimensions are presented in Fig. 1 (Right hand panel) in the form of a heat map.

Having described the different dimensions that make up the experiential reports in the episodic imagination task, we explored how these loadings varied across the task conditions. These data are presented in Fig. 2 and were analysed using a within participant analysis of variance (ANOVA) with repeated measures on temporal distance (Near and Far) and direction (Past and Future).

For immersive thoughts the effect of direction was not significant [$F(1,146) = .06, p = .80$] while the main effect of distance was [$F(1,146) = 12.66, p = .001$]. It can be seen in Fig. 2 that the effect of temporal distance is most pronounced for retrospective experiences, with the most immersive experiences associated with the more distant past. The Distance × Direction interaction approached significance [$F(1,146) = 3.57, p = .061$]. Paired t-tests comparing the difference between near and far experiences in the past revealed a significant difference [$t(146) = -3.91, p < .001$]. No difference was observed for experiences focused on the future [$t(146) = -1.04, p = .303$].

Analysis of the Modality of experience yielded an effect of direction [$F(1,146) = 21.93, p < .001$] and an effect of distance [$F(1,146) = 8.4, p < .005$]. The distance by direction interaction was at trend level [$F(1,146) = 3.53, p = .059$]. The effect of
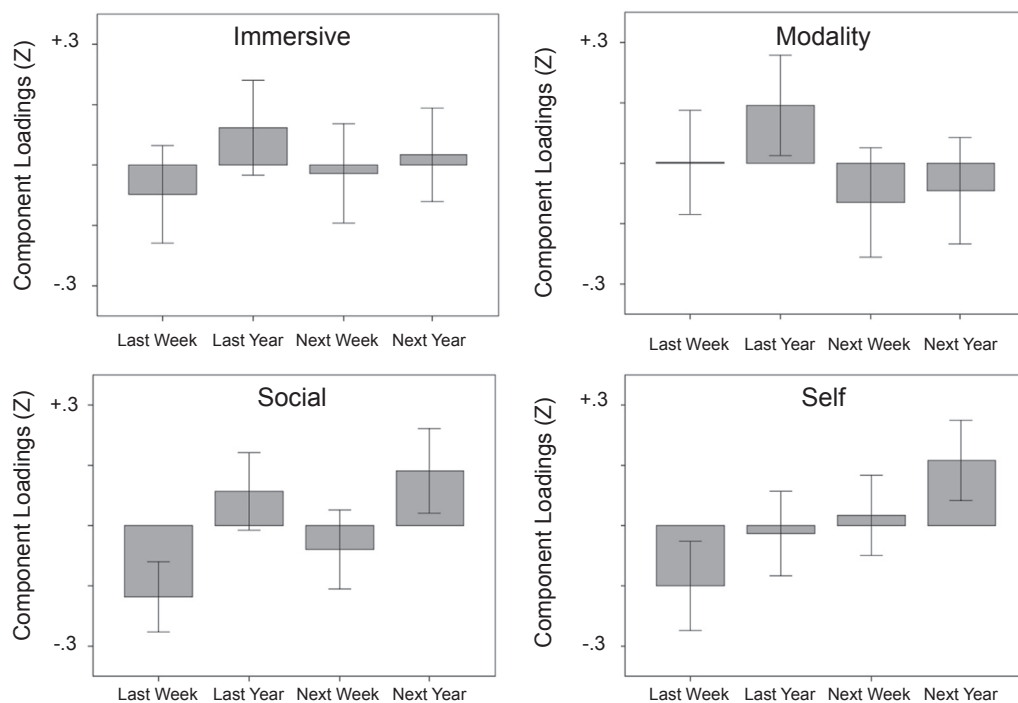

Fig. 2 — Distribution of the different components of simulated experience across different temporal periods. Separate plots reflect the variation of the components across each condition of our experiment. The error bars display the 95% confidence intervals of the mean.

temporal distance was most apparent for experiences in the past, with near past experiences characterized as more visual in character. Paired t-tests indicated the difference in modality was significant for experiences focused on the past [$t(146) = -2.35$, $p < .05$] but not for the future [$t(146) = -1.60$, $p < .05$].

Analysis of the Social dimension to experience indicated a significant effect of distance [$F(1,146) = 28.74$, $p < .001$] with experiences that were more distant more social. The effect of direction was at trend level [$F(1,146) = 3.57$, $p = .06$] with experiences more social for the future than the past. The interaction was not significant [$F(1,146) = .66$, $p = .417$].

For the dimension of self both the main effect of direction [$F(1,146) = 24.16$, $p < .001$] and distance [$F(1,146) = 10.9$, $p < .001$] were significant. Experiences about the future loaded more on the self than did those of the past. Experiences were also described as more related to the self if they were more distant in time than if they were closer.

3.2. Functional connectivity analyses

We explored whether individual variation in patterns of functional connectivity from uni-modal regions of visual and auditory cortex was associated with different types of imaginative thoughts. We conducted a multiple regression in which the dependent variables were the spatial maps describing the functional connectivity of the visual seed. The explanatory variables were the individual loadings describing the weightings of each component for each task separated into each of the four conditions of the experiment (Distant Past, Near Past, Distant Future, Near Future). Our analysis failed to identify any significant patterns of functional connectivity from auditory cortex that were related to patterns of imagination and therefore we focus on the results identified from seeding the visual network. The unthresholded maps from all analyses are available on Neurovault in the collection associated with this paper.

Analysis of the spatial maps produced by seeding visual cortex revealed a single result that passed our cut-off for multiple comparisons, indicating stronger functional connectivity between the visual cortex and a region of posterior cingulate/retrosplenial cortex (RSPC) for individuals whose simulations of next year tended to be more positive and social (see Fig. 3). In this figure it can be seen that a region of retrosplenial cortex/posterior cingulate cortex shows stronger coupling with primary unimodal cortex (presented in green in the sub panel). The scatter plot describes the relationship between functional connectivity and the propensity for social experiences when imagining the distant future. This analysis indicates patterns of functional connectivity implicating interactions between visual cortex with RSPC in aspects of imagination that emphasize positive social thoughts about the future. To ensure that this result was not a result of the confounding effect of motion we reran the analyses including motion as a nuisance co-variate at the group level yielding comparable results (see Supplementary Fig. 2).

Having identified a pattern of functional connectivity linking visual cortex to a region of RSPC, we next sought to contrast the target region's connectivity with that of the seed region. We used the cluster generated by the prior analytic step as a seed to drive a functional connectivity analysis in an independent data set (see Methods). We also seeded the same visual network seed in this new group of participants. The resulting maps were compared in Fig. 4. While the connectivity of the visual region is largely restricted to posterior visual-related areas, including central and lateral occipital regions, the connectivity of the RSPC shows a much more widely distributed connectivity pattern, corresponding not only to the adjacent visual cortex, but also to many of the regions that make up the DMN. These regions include the inferior parietal lobe/angular gyrus, posterior cingulate cortex, hippocampus, anterior temporal lobe and the medial prefrontal cortex. Together these analyses suggest that activity in visual cortex is correlated with activity in the RSPC, while the
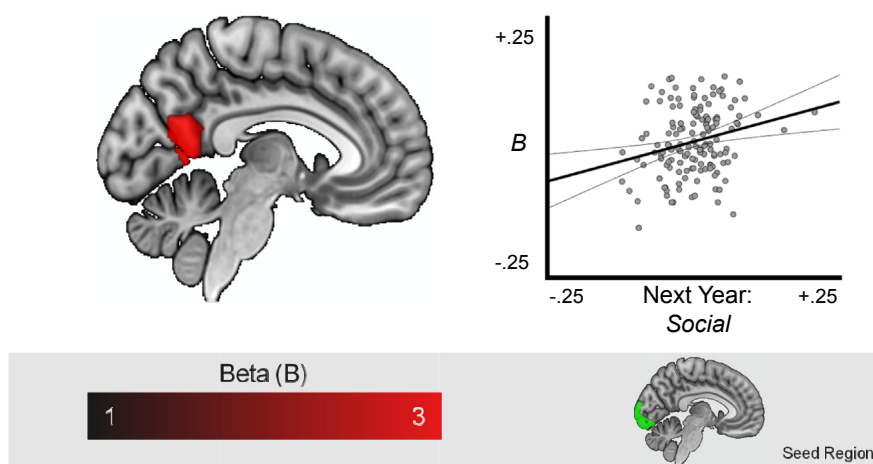

Fig. 3 — Functional connectivity of the visual cortex linked to individual variation in the features of directed episodic thoughts. The region in red indicates regions displaying connectivity with the visual cortex that was stronger for participants whose distant future thoughts loaded on social content. The scatterplot presents the individual variation on which this analysis is based. Each point describes each participant. The error lines on the scatterplot indicate the 95% confidence estimates of the mean. All maps are thresholded at Z = 2.6 and corrected for multiple comparisons accounting for the number of voxel in the brain and the number of seed regions investigated. Beta reflects the parameter estimates.
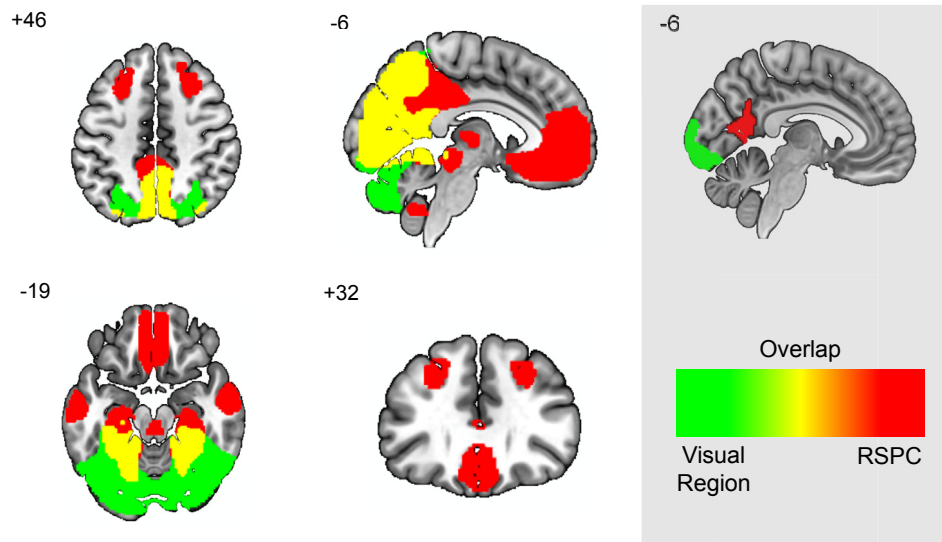
Fig. 4 — Similarities and differences in the connectivity of the visual cortex and retrosplenial cortex. Functional connectivity of the retrosplenial cortex (regions in red) and the visual cortex (regions in green). Regions in yellow indicate regions of overlap. These maps are fully saturated to emphasize the regions of overlap. All maps are thresholded at Z = 2.6 and corrected for multiple comparisons accounting for the number of voxel in the brain. Numbers at the top left of each panel indicates the coordinate value of the corresponding plane. Right Panel (highlighted in grey) shows the seed regions used for the visual cortex and RSPC.

RSPC has a pattern of temporal correlation with core regions of the DMN. To ensure comparability of the retrosplenial connectivity across data sets we show the commonality in pattern between the two data sets in Supplementary Fig. 3, where it can be seen that broadly comparable patterns are present in both data sets.

Our final analysis examines whether the propensity for coupling with the visual cortex is a general property of all regions of the DMN, or whether this is specific to certain nodes within this network such as the RSPC. We contrasted the connectivity of the RSPC identified in the current experiment with a cluster defined in a prior resting-state studies that found that different types of spontaneous thoughts converged in an anterior region of the DMN in medial prefrontal cortex (Smallwood et al., 2016). We calculated the differential functional connectivity of these two regions (see Fig. 5). The region of RSPC showed relatively greater functional connectivity with adjacent regions of cortex, including the angular gyrus and the medial temporal lobe, as well as stronger connectivity with bilateral regions of dorso-lateral prefrontal cortex. In contrast, the medial prefrontal cortex (mPFC) showed stronger connectivity to regions of adjacent lateral and medial prefrontal cortices, as well as to dorso-lateral parietal regions including the intraparietal sulcus and the motor cortex. Meta-analytic decoding of these differences in functional connectivity linked the retrosplenial cortex to functions such as "navigation", "scenes" and "episodic memory", and medial prefrontal cortex to "motor", "working memory", "language" and "comprehension". As with our other analyses we present a comparison of the differential seeding in both data sets in Supplementary Fig. 4 where it can be seen that the same spatial pattern is present in both samples.

4.   Discussion

In the present study we sought to test whether connectivity between visual and auditory cortex with regions of the DMN is associated with aspects of imaginative thought. We found that distant future thoughts tended to be characterized as positive and social in nature than past thought. Moreover, the more an individual embodied this propensity, the stronger intrinsic communication was between visual and retrosplenial cortex/posterior cingulate cortex. We explored the connectivity of the cluster identified in the retrosplenial cortex in an independent data set, finding patterns of connectivity encompassing both regions of visual cortex, as well as those of the DMN. Finally, we compared the connectivity of the retrosplenial cortex identified in this experiment, with a region of medial prefrontal cortex implicated in spontaneous thoughts about the future in a prior study. This analysis shows stronger functional coupling between retrosplenial and visual cortex, medial and lateral temporal lobe and angular gyrus, while the medial prefrontal cortex was more coupled to intraparietal sulcus, ventro-lateral prefrontal cortex and primary and supplementary motor regions.

Our results suggest that retrosplenial cortex may interact with visual cortex to facilitate features of social imagination about the distant future. Task based studies show that the retrosplenial cortex is active during future thinking (e.g., Addis et al., 2007; Okuda et al., 2003; Szpunar et al., 2007), a pattern often interpreted as reflecting the process of "scene construction" (mentally generating and maintaining a complex and coherent scene or event) (Hassabis & Maguire, 2007). According to this view, retrosplenial cortex links with
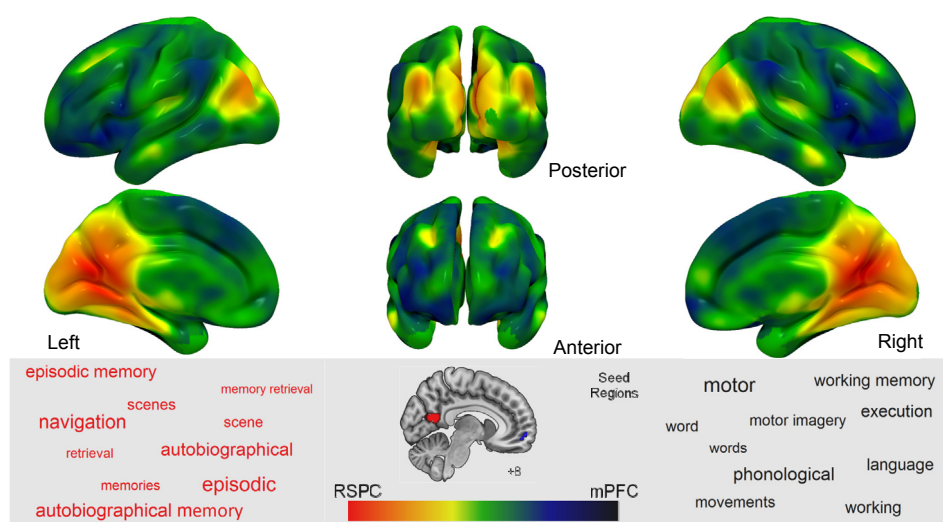
Fig. 5 — *Differences in connectivity of regions of retrosplenial cortex and medial prefrontal cortex implicated in imaginative thought. The spatial maps describe patterns of relative differences in connectivity between the retrosplenial and medial prefrontal cortex. The word clouds are generated using Neurosynth and reflect the top ten items associated with each end of the connectivity spectrum.*

hippocampus provide a visuo-spatial context into which disparate representations are bound together (Hassabis et al., 2007a, 2007b). This allows novel experiences, such as thoughts about the future, to be generated (Addis et al., 2007; Summerfield et al., 2010). Our analysis, based on patterns of intrinsic connectivity, experiential data and meta-analytic decoding, suggests that interactions between visual and retrosplenial cortex provide a mechanism through which aspects of imagination harness the process of scene construction. Notably a recent study has shown that medial regions of visual cortex, as well as posterior hippocampal regions adjacent to the retrosplenial cortex, are activated in transient fashion when participants simulate the future (Thakral et al., 2017). It is possible that our observation of increased connectivity between visual cortex and retrosplenial cortex is important in the construction of an imagined future event rather than its maintenance.

Although these data highlight a role for interactions between retrosplenial cortex and visual cortex during imagination, there are a number of important considerations that should be borne in mind when considering these results. First, our analysis exploits trait differences in brain organization at rest, to understand the neural processes that take place when we think about the future (a state). This analytic approach may bias our findings towards patterns that reflect traits rather than states. However, task based studies, which are more direct measures of underlying processes, show activation in retrosplenial cortex when we think about the future (Addis et al., 2007; Okuda et al., 2003; Szpunar et al., 2007) making this less likely. Nonetheless it will be important to assess the connectivity between visual cortex and retrosplenial cortex during future thinking in an online task. Second, although our study links the capacity to imagine the future to interactions between visual and retrosplenial cortex, it is less clear what aspects of prospective experience this process reflects. Distant prospective social thoughts may be

unique in many dimensions, such as their relationship to goals (D'Argembeau et al., 2010; D'Argembeau & Mathy, 2011); they may also vary on their level of construal (Trope & Liberman, 2010). Moreover, cortical hubs, like the retrosplenial cortex, are likely to be involved in multiple different types of cognition. For example studies have shown that the retrosplenial cortex is important for navigation (Epstein, 2008), the storage and retrieval of spatial information (Czajkowski et al., 2014). Third, it will be important for future studies to explore connectivity between visual and retrosplenial cortex when participants engage in different types of imagination and to compare the similarities and differences in the resultant patterns. It is also unclear from our current data whether we can dismiss a role of auditory processing in future thinking. View of prospection often emphasizes the potential for language processing to scaffold thought (Suddendorf & Corballis, 1997), and it is possible that this would be supported in part through interactions with auditory cortex. A study that probed different aspects of experience, or that induced different types of imaginative thought, could reveal that integration of information from the auditory cortex would be important for types of imagination such as inner speech (Alderson-Day & Fernyhough, 2015). Fourth, individual differences in resting state have been linked to measures of cognitive functioning in multi domains including intelligence (Finn et al., 2015) and life style features (Smith, 2016). It is not currently known whether the results obtained from these analyses emerge from patterns of thoughts that participants experience during the resting state session, or reflect more basic features of the underlying neurocognitive architecture. In our study, for example, it is possible that participants who tend to engage in social thoughts about the future at rest, also tended to generate these types of experiences during our task. To identify the mechanism upon which these functional connectivity relationships depend, it will be necessary for future studies to identify those aspects of ongoing neural

activity that are linked to experience during the resting state and identify whether these predict laboratory measures. Fifth, we did not acquire open ended descriptions of the participants experience during the laboratory session. This would have allowed independent raters to evaluate the characteristics of each thought more objectively by using a common scale. Finally, our study used large scale networks from a comprehensive decomposition of resting-state data (Yeo et al., 2011). This seed region, therefore, captures a meaningful function unit, yet one that encompasses many different sub regions. Future studies could profit from exploring whether neural signals from different regions of visual or auditory cortex contributes in a differential manner to imaginative thought.

In conclusion, our study has shown that individual differences in connectivity between retrosplenial and visual cortex is correlated with the variation in the propensity for social information when we consider the distant future. This pattern is consistent with retrosplenial cortex, in conjunction with the hippocampus, acting as a hub, playing an integrative role in scene construction during prospection. We suspect other DMN regions may play complimentary roles in other aspects of imaginative thought. Our meta-analytic decoding suggests that another DMN region, within medial prefrontal cortex, is important for functions linked to language and working memory. Other DMN regions, like anterior temporal lobe, bind multimodal information together to provide abstract conceptual representations (Murphy et al., 2017; Visser et al., 2010, 2012). Decoding the relative connectivity of an inferior cluster within anterior temporal lobe in one of our prior studies, revealed terms such as "comprehension", "semantics" and "social processing" (Murphy et al., 2017). In another previous study, we found that interactions between the left anterior lobe and the left inferior frontal gyrus at rest are important for thematic aspects of spontaneous thoughts (Vatansever et al., 2017). Together these data provide converging evidence that functional connectivity can be heterogeneous for different nodes in the DMN, and that these patterns may underpin different aspects of imagination. We speculate that this capacity to integrate information from different regions of cortex within a single network may be an important clue to understanding the role the DMN plays in creating the landscape within which imaginative experiences unfold.

Conflict of interest

The authors declare no competing financial interests.

Acknowledgements

Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.cortex.2017.11.015.

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