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Tracking thoughts: Exploring the neural architecture of mental time travel during mind-wandering

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ABSTRACT

The capacity to imagine situations that have already happened or fictitious events that may take place in the future is known as mental time travel (MTT). Studies have shown that MTT is an important aspect of spontaneous thought, yet we lack a clear understanding of how the neurocognitive architecture of the brain constrains this element of human cognition. Previous functional magnetic resonance imaging (MRI) studies have shown that MTT involves the coordination between multiple regions that include mesiotemporal structures such as the hippocampus, as well as prefrontal and parietal regions commonly associated with the default mode network (DMN). The current study used a multimodal neuroimaging approach to identify the structural and functional brain organisation that underlies individual differences in the capacity to spontaneously engage in MTT. Using regionally unconstrained diffusion tractography analysis, we found increased diffusion anisotropy in right lateralised temporo-limbic, corticospinal, inferior fronto-occipital tracts in participants who reported greater MTT. Probabilistic connectivity mapping revealed a significantly higher connection probability of the right hippocampus with these tracts. Resting-state functional MRI connectivity analysis using the right hippocampus as a seed region revealed greater functional coupling to the anterior regions of the DMN with increasing levels of MTT. These findings demonstrate that the interactions between the hippocampus and regions of the cortex underlie the capacity to engage in MTT, and support contemporary theoretical accounts that suggest that the integration of the hippocampus with the DMN provides the neurocognitive landscape that allows us to imagine distant times and places.

1. Introduction

Conscious experience is not restricted to events in the here and now. The prominence of states such as daydreaming and mind-wandering in our mental lives illustrates that we often mentally escape from the constraints of the moment and generate thoughts regarding people, places and situations other than those in the immediate environment (Killingsworth and Gilbert, 2010). It is now known that these states are accompanied by a measurable reduction in the processing of external events, indicating a disengagement, or decoupling, of attention from the external environment (Smallwood et al., 2008). Instead of relying on perceptual input for their mental content, it is hypothesised that these experiences are built almost exclusively from representations in semantic and episodic memory (see Smallwood and Schooler (2015) for a review).

Evidence from functional neuroimaging is consistent with the view that memory retrieval is a core process with which we generate spontaneous thought. Prior work has demonstrated that a large-scale brain system known as the default mode network (DMN) is important for the thoughts that are generated during the mind-wandering state (Mason et al., 2007; Christoff et al., 2009). The DMN is generally identified as a distributed regional assembly anchored by hubs in the medial prefrontal cortex, the posterior cingulate cortex and the angular gyrus (Raichle et al., 2001; Raichle, 2015). During tasks that involve retrieving information from memory, the DMN often integrates information from medial and lateral temporal regions known to play a pivotal role in episodic and semantic memory, such as the hippocampus (Sestieri et al., 2011) and the anterior temporal lobe (Patterson et al., 2007). Several studies have linked the DMN, as well as related structures such as the hippocampus, to processes such as imagining events from the future or past (Schacter et al., 2007), which are collectively known as mental time travel (MTT). Studies have shown that MTT is an important element of the mind-wandering state (Smallwood et al., 2009b; Baird et al., 2011) and a meta analytic study has shown similarities between the neural activation during mind-wandering and episodic future thinking (Stawarczyk and D'Argembeau,

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2015). A recent study (Ellamil et al., 2016) has also indicated that the hippocampus is activated early during the spontaneous generation of thoughts while mind-wandering.

Although previous functional magnetic resonance imaging (MRI) studies have established a functional role of the DMN in the mind-wandering state (Mason et al., 2007; Allen et al., 2013; Ellamil et al., 2016), the extent to which the neural architecture of this network and associated regions of cortex constrain naturally occurring spontaneous thought remains uncertain. In the current study, we tested the hypothesis that variations in spontaneous thoughts across participants emerge as a consequence of the large-scale structural network organisation of the brain. We applied regionally unconstrained tractography analysis to diffusion magnetic resonance imaging data in a cohort of healthy adults and assessed whether individual variability in the contents of their thoughts related to markers of structural connectivity. Our analysis approach was complemented with probabilistic connectivity mapping, to identify the cortical grey matter with the highest connection probability to these tracts. Finally, we used seed-based resting-state functional MRI connectivity mapping to identify associated functional networks. Based on functional studies of the role of the DMN and regions in the medial and lateral temporal lobe in thoughts generated during the mind-wandering state (Christoff et al., 2009; Stawarczyk et al., 2011), we anticipated our structural analysis to highlight a constellation of regions, including the medial prefrontal, posterior cingulate, as well as lateral and medial temporal cortices, including the hippocampus.

2. Methods

2.1. Participants

A total of 86 healthy participants were recruited by advert from the Department of Psychology at the University of York (51 women, age range 18–31). They were offered either a payment of £20 or a commensurate amount of course credits. Written consent was obtained for all participants and the study was approved by the York Neuroimaging Centre Ethics Committee. Participants were recruited in two cohorts (Sample A, n=47; Sample B, n=39) in different time periods, although there were no differences relevant to the study. While both samples participated in the behavioural session and underwent a resting state (rs) functional MRI scan, we acquired diffusion MRI data only for sample A. We excluded 8 out of 39 participants from Sample B due to incomplete brain coverage (whole-brain coverage <94%). Having two samples gave us the opportunity to treat them separately in our analyses and investigate the robustness of our behavioural and functional MRI results. The behavioural and functional MRI data in this study are the same as those reported in Smallwood et al. (2016).

2.1.1. Independent sample

We also used an independent dataset to provide independent confirmation of functional connectivity results. These data were obtained from a publicly available dataset: the Nathan Kline Institute (NKI)/Rockland Enhanced Sample and contained 141 subjects. Full details of this sample can be found in Gorgolewski et al. (2014).

2.2. Behavioural methods

2.2.1. Choice reaction time task

To acquire information about the content of spontaneous thought in a situation conducive to the mind-wandering state, participants performed a simple non-demanding choice reaction time task. This task is routinely used in studies of spontaneous thought because it creates periods when spontaneous thoughts are generated with as similar a frequency as when participants are not engaging in a task (Smallwood et al., 2009b). Participants sat in a testing booth and were asked to make a parity judgement to numerals that were coloured red. These stimuli were presented in a stream of non-coloured numerals, to which no response was required. Stimuli were presented with a slow inter-stimulus interval (2200–4400 ms) and remained on screen for 1000 ms. The task lasted 15 min and participants performed a single run. The occurrence of the target and non-target stimuli was randomly determined with a mean target number of M=25.2, SE=0.6 and a mean non-target number of M=109.6, SE=1.1. Participants responded by using the mouse button. Accuracy was high (mean ± SD=0.93 ± 0.08), with a mean response time of 900 ms (SD=161). Participants performed this task in a laboratory testing session, scheduled one day after the scanning.

2.2.2. Multi-dimensional experience sampling (MDES)

At unpredictable moments while performing the laboratory task, participants were interrupted and asked to rate different aspects of their experience. They were asked to focus their answers on the contents of their experience the moment immediately prior to the interruption, thereby reducing demands on memory. They responded using a continuous Likert scale. The specific questions used are described in Table 1 and they were all asked during each probing. They were selected from prior studies (Smallwood et al., 2016) and examined the content of thoughts (e.g. temporal content relating to the past or future, referent of thought - themselves or another person - and emotional valence), as well as the form these thoughts took (whether the thoughts were in words or images, the level of detail and intrusiveness, etc.).

Whenever experience sampling occurred, the questions were administered in a quasi-random order. The first question was always about task focus, followed by blocks of questions about the content and form of thoughts. On each occasion, the order of each block, as well as the order of questions within each block, was randomised. Participants were probed an average of 8 times during the fifteen-minute task. We used a fully randomised sequence of experience sampling probes to ensure that regularities in our probing schedule did not bias the results of our experiment (Seli et al., 2013).

As in previous studies, data from each individual was concatenated into a single matrix. We z-scored the data from each sample separately to minimise differences between them, and fed them into a principal component analysis (PCA) with varimax rotation, allowing patterns of covariance that broadly correspond to different types of thought to be identified. The decomposition of these data, as well as a replication sample, has previously been reported by Smallwood et al. (2016). The decomposition was performed in separate analyses, one for the content of the experience and one for the form. We chose to decompose the components of content and form separately because our method of experience sampling presented them in these conceptual groups, reflecting our a priori interest in decomposing them as separate factors. In addition, we have successfully employed this technique of experience sampling in several prior studies (Ruby et al., 2013a,b; Engert et al., 2014; Medea et al., 2016) and applying the same procedure in the current study provided the chance to relate our data to these prior

Table 1
Experience sampling questions used in this experiment.

Dimension	Question (My thoughts...)	Left	Right
Task	... were focused on the task I was performing	Not at all	Completely
Future	... involved future events	Not at all	Completely
Past	... involved past events	Not at all	Completely
Self	... involved myself	Not at all	Completely
Other	... involved other people	Not at all	Completely
Emotion	The content of... was	Negative	Positive
Images	... were in the form of images	Not at all	Completely
Words	... were in the form of words	Not at all	Completely
Intrusive	... were intrusive	Not at all	Completely
Detail	... were vague and non-specific	Not at all	Completely

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