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DISSERTATION

Structural and functional brain organization underlying
spontaneous and deliberate mind-wandering

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Abstract

Immer wieder erleben wir, dass wir mit den Gedanken von unserer aktuellen äußeren Umgebung abschweifen. Gegenstand psychologischer und neurowissenschaftlicher Debatten ist dabei die Frage, inwiefern das auftretende Abschweifen der Gedanken in Beziehung zu kognitiver Kontrolle steht. Einander gegenüberstehende Positionen umfassen dabei sowohl die Perspektive, dass ein zeitweises Aussetzen kognitiver Kontrolle Perioden des Gedankenabschweifens ermöglicht, aber auch, dass kognitive Kontrolle bei der Stabilisierung selbst-generierter Gedankeninhalte hilfreich ist. Ein vielversprechender Ansatz, der zur Klärung der kontroversen Beziehung zwischen dem Gedankenabschweifen und exekutiver Kontrolle beitragen könnte, liegt in der Berücksichtigung des Ausmaßes an Intentionalität, mit dem das Gedankenabschweifen erlebt wird. Mittels der Untersuchung der strukturellen und funktionellen Gehirnorganisation, die den Arten des willkürlichen und spontanen Gedankenabschweifens zugrunde liegt, ist es das Ziel der vorliegenden Arbeit, die komplexe Beziehung zwischen dem Gedankenabschweifen und kognitiver Kontrolle aufzuklären.

Zu diesem Zweck wurden die kortikale Dicke und funktionelle Konnektivität im Zusammenhang mit Selbstauskunftsmaßen analysiert, welche die generelle Tendenz des erlebten willentlichen und spontanen Gedankenabschweifens quantifizieren. Konkret wurde dabei untersucht, (i) ob interindividuelle Unterschiede bezüglich der zwei Arten des Gedankenabschweifens Varianz in der kortikalen Dicke erklären und (ii) inwiefern die zwei Arten des Gedankenabschweifens die funktionellen Konnektivitätsprofile von Schlüsselregionen des fronto-parietalen Netzwerks (FPN) modulieren, welches eine zentrale Stellung in der exekutiven Kontrolle einnimmt.

Im Zusammenhang mit einer erhöhten Tendenz zum willkürlich erlebten Gedankenabschweifen zeigte sich eine größere kortikale Dicke sowie erhöhte funktionelle Konnektivität vom inferioren frontalen Sulcus überwiegend in präfrontalen Regionen. Diese Regionen überlappen ihrerseits mit Arealen des FPNs und Default-Mode Netzwerks (DMN), wobei letzteres gemeinhin mit dem Gedankenabschweifen assoziiert ist. Im Gegensatz dazu waren höhere Neigungen zum spontanen Gedankenabschweifen mit einer geringer ausgeprägten kortikalen Dicke in parietalen und posterior-temporalen Regionen zu beobachten, insbesondere

an den Schnittstellen zwischen FPN und DMN. Darüber hinaus zeigte sich eine erhöhte funktionelle Konnektivität zwischen dem intraparietalen Sulcus und dem ventralen inferioren frontalen Gyrus, der mit Regionen des DMNs und limbischen Netzwerks überlappt.

Zusammengefasst zeigt diese Arbeit, dass Formen des willkürlichen und spontanen Gedankenabschweifens auch auf Basis der zugrunde liegenden strukturellen und funktionellen Gehirnorganisation differenzierbar sind. Dabei legen die Ergebnisse nahe, dass sich das Ausmaß an Intentionalität in dem Integrationsgrad zwischen FPN und DMN widerspiegelt, wobei eine ausgeprägtere Integrität mit einem erhöhten Grad an Intentionalität während des Gedankenabschweifens assoziiert ist. Insofern heben die Resultate nicht nur die Relevanz exekutiver Kontrolle bezüglich adaptiver external *und* internal ausgerichteter Kognitionen hervor, sondern unterstreichen grundsätzlich auch die Notwendigkeit einer nuancierten Betrachtung des Phänomens des Gedankenabschweifens.

Abstract (Englisch)

Every so often we find our minds wandering away from our current external environment. Understanding how this experience relates to cognitive control has become an important matter of psychological and neuroscientific debate. Opposing arguments include both the perspective that failures in cognitive control enable subsequent periods of mind-wandering, and that cognitive control helps stabilizing the self-generated mental content. One promising view that could clarify the controversial relationship between mind-wandering and executive control, however, might lie in considering the level of intentionality with which we engage in self-generated thought. By investigating the underlying structural and functional brain organization of spontaneous and deliberate forms of mind-wandering, the current thesis aims to disentangle the complex relationship between mind-wandering and the control of cognition.

To this end, cortical thickness as well as seed-based functional connectivity analysis was related to a self-report measure that quantifies trait level tendencies to experience spontaneous and deliberate forms of mind-wandering. It specifically was examined (i) if interindividual differences in the two types of mind-wandering explain variance in cortical thickness, and (ii) how these types of mind-wandering modulate the functional connectivity profiles of key regions of the fronto-parietal network (FPN), which is implicated in executive control.

With respect to higher rates of deliberate mind-wandering, increased cortical thickness and elevated functional connectivity from the inferior frontal sulcus was primarily observed in prefrontal regions. These regions overlap with areas of the FPN and default-mode network (DMN), the latter being commonly associated with mind-wandering. In contrast, elevated rates of spontaneous mind-wandering were associated with decreased cortical thickness in parietal and posterior temporal regions that fall at the intersection of the FPN and DMN. Functional connectivity was increased between intraparietal sulcus and ventral inferior frontal gyrus, which overlaps with limbic and default-mode regions.

In conclusion, this thesis provides evidence that deliberate and spontaneous mind-wandering are differentiable in terms of their underlying structural and functional brain organization. Specifically, the results suggest that the extent of intentionality in the mind-wandering state is reflected by the level of integration between the FPN and DMN, such that higher integrity is associated with the experience of a higher degree of deliberation during the mind-wandering state. This not only underpins the importance of executive control in both adaptive externally *and* internally directed cognition but also calls for a nuanced perspective towards the mind-wandering state in general.

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„Ich, Johannes Golchert, versichere an Eides statt durch meine eigenhändige Unterschrift, dass ich die vorgelegte Dissertation mit dem Thema: „Structural and functional brain organization underlying spontaneous and deliberate mind-wandering“ selbstständig und ohne nicht offengelegte Hilfe Dritter verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel genutzt habe.

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Datum

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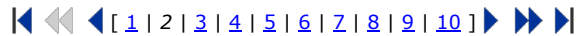
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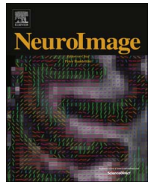
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Individual variation in intentionality in the mind-wandering state is reflected in the integration of the default-mode, fronto-parietal, and limbic networks



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ABSTRACT

Mind-wandering has a controversial relationship with cognitive control. Existing psychological evidence supports the hypothesis that episodes of mind-wandering reflect a failure to constrain thinking to task-relevant material, as well as the apparently alternative view that control can facilitate the expression of self-generated mental content. We assessed whether this apparent contradiction arises because of a failure to consider differences in the types of thoughts that occur during mind-wandering, and in particular, the associated level of intentionality. Using multi-modal magnetic resonance imaging (MRI) analysis, we examined the cortical organisation that underlies inter-individual differences in descriptions of the spontaneous or deliberate nature of mind-wandering. Cortical thickness, as well as functional connectivity analyses, implicated regions relevant to cognitive control and regions of the default-mode network for individuals who reported high rates of deliberate mind-wandering. In contrast, higher reports of spontaneous mind-wandering were associated with cortical thinning in parietal and posterior temporal regions in the left hemisphere (which are important in the control of cognition and attention) as well as heightened connectivity between the intraparietal sulcus and a region that spanned limbic and default-mode regions in the ventral inferior frontal gyrus. Finally, we observed a dissociation in the thickness of the retrosplenial cortex/lingual gyrus, with higher reports of spontaneous mind-wandering being associated with thickening in the left hemisphere, and higher reports of deliberate mind-wandering with thinning in the right hemisphere. These results suggest that the intentionality of the mind-wandering state depends on integration between the control and default-mode networks, with more deliberation being associated with greater integration between these systems. We conclude that one reason why mind-wandering has a controversial relationship with control is because it depends on whether the thoughts emerge in a deliberate or spontaneous fashion.

1. Introduction

Conscious experience is not always tethered to the events taking place in the here and now: Indeed, in daily life, people's minds frequently wander away from the external environment toward inner musings (Kane et al., 2007; Killingsworth and Gilbert, 2010). One

enduring puzzle concerning this common form of everyday thought is how it relates to cognitive control. Studies from multiple research groups have shown that people with low levels of control often experience relatively high rates of mind-wandering compared with people who have high levels of control (McVay and Kane, 2009; Mrazek et al., 2012; Unsworth and Mcmillan, 2013). However, this relationship

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is not consistently observed across task contexts. Indeed, research has shown that people with relatively high levels of control tend to engage in *more* mind-wandering during easy tasks than do people with relatively low control (e.g. Bernhardt et al., 2014; Levinson and Davidson, 2012; Rummel and Boywitt, 2014; Smallwood et al., 2013), presumably because (a) easy tasks afford people the opportunity to mind-wander without incurring performance costs, and (b) high-control individuals are better able to modulate their mind-wandering in accordance with task demands. Accordingly, it has been proposed that understanding the relationship between mind-wandering and control needs to take into account the ongoing task context as well as the nature of the mental content that occurs during the mind-wandering state (Smallwood and Andrews-Hanna, 2013; Smallwood and Schooler, 2015).

It has recently been suggested that one important aspect of mind-wandering is whether it is experienced as occurring deliberately or spontaneously (e.g. Seli et al., 2016b). Studies have found that individuals who report high levels of spontaneous mind-wandering in everyday life tend to score higher on measures of attention-deficit/hyperactivity disorder (ADHD; Seli et al., 2015b), obsessive-compulsive disorder (OCD; Seli et al., 2016a), and that they are more reactive to their inner experiences (Seli et al., 2015a). More recently, it has not only been shown that both types of mind-wandering are related to their corresponding state-levels when assessed in the laboratory (Seli et al., 2016c) – which indicates that the measures of spontaneous and deliberate mind-wandering have construct validity – but also that during easy tasks, deliberate mind-wandering is more frequently reported than is spontaneous mind-wandering (Seli et al., 2016b). The association between spontaneous mind-wandering and less controlled thought and behaviour, as well as the high incidence of deliberate mind-wandering during easy tasks, both raise the possibility that the difference between spontaneous and deliberate mind-wandering arises through differences in how these two mental experiences relate to cognitive control.

Confusion regarding how experiences such as mind-wandering relate to the control of cognition extends to the default-mode network (DMN), a neural system that has been suggested to be the basis of many features of the mind-wandering state (Fox et al., 2015; Gusnard and Raichle, 2001; Raichle et al., 2001). This large-scale network engages a constellation of regions including the medial prefrontal cortex, posterior cingulate cortex, regions of the angular gyrus, and anterior as well as medial aspects of the temporal lobe. Early interpretations of the functions of the DMN focused on its tendency to deactivate during demanding tasks (e.g. Raichle et al., 2001), as well as its anti-correlation with regions that are commonly activated during externally oriented tasks, such as the dorsolateral prefrontal cortex (Fox et al., 2005). These observations have led to conceptualizations of the role of the DMN in cognition as supporting automatic or self-relevant information processing (c.f. Anticevic et al., 2012; Hamilton et al., 2015). In addition, the DMN is generally contrasted with networks that are activated during demanding tasks, and which are important in the control of cognition, such as the fronto-parietal network (FPN; Cole et al., 2013; Duncan, 2010; Fedorenko et al., 2013).

It is often assumed that the DMN works in opposition to networks that support more controlled cognition (e.g. Anderson et al., 2016; Hellyer et al., 2014). However, recent studies have challenged this dichotomous view of DMN function, indicating that this network can play a role in active cognitive processing during demanding tasks. It is now thought that the DMN contributes to complex tasks by increasing connectivity with regions supporting cognitive control (e.g. Krieger-Redwood et al., 2016; Piccoli et al., 2015; Spreng et al., 2014, 2010; Vatansever et al., 2015). These findings suggest that, despite evidence of an anti-correlation between the DMN and executive control systems at rest, there are functionally significant interactions between these systems that allow information from memory to make a contribution to

a controlled train of thought. Critically, these findings support a hypothesised role for both of these systems when internal thought has a controlled or deliberate nature (see Smallwood et al. (2011) and Spreng (2012)). Given the evidence indicating that the DMN is active during mind-wandering (Allen et al., 2013; Christoff et al., 2009; Mason et al., 2007; Stawarczyk et al., 2011), it is possible that its interactions with systems such as the FPN may provide a mechanism through which experiences that occur during mind-wandering may be organised in a manner that is more closely aligned with a person's intentions (Fox et al., 2015; Seli et al., 2016d; Smallwood et al., 2012).

The current study used magnetic resonance imaging (MRI) to explore the hypothesis that the intentionality associated with the mind-wandering state depends on the brain's ability to integrate information from the DMN and the FPN. To do this, in a single session, we measured the structural and functional brain organisation of a large cohort of participants who had completed validated measures (Seli et al., 2016c) of spontaneous and deliberate mind-wandering (Carriere et al., 2013), which assess the rate at which people engage in these two types of mind-wandering in their daily lives. This design allowed us to test the neurocognitive architecture that underlies trait-level variation in the amount of deliberation in mind-wandering in two complementary ways. First, we performed a surface-wide cortical-thickness analysis to identify how variation in the grey-matter structure of the cortex relates to people's propensity to engage in deliberate and spontaneous mind-wandering. Second, we used seed-based functional connectivity to explore the function of sites with well-established roles in cognitive control: the inferior frontal sulcus, the intraparietal sulcus, and the pre-supplementary motor area, all of which are key nodes of the FPN (for a review see Duncan (2010)). We focused on regions in the frontal-parietal control system since, according to component-process accounts of the mind-wandering state (e.g. Smallwood, 2013, Smallwood and Schooler, 2015), these would provide the greatest chance to dissociate spontaneous and deliberate types of mind-wandering. If deliberate mind-wandering depends on the integration of the DMN and the FPN (Smallwood et al., 2011), then we expected to find that people who report more deliberate mind-wandering would have greater cortical thickness at the intersection of these two networks and greater functional integration between them. Based on the hypothesis that spontaneous mind-wandering may often result from problems in control, we expected that this form of mind-wandering would not be associated with greater cortical thickness in areas associated with cognitive control, or to be associated with as clear a pattern of coupling between the DMN and the FPN.

2. Method

2.1. Participants

We analyzed data from 123 healthy volunteers (age: $M=26.59$, $SD=4.23$; 59 females) who were part of a larger cross-sectional data-collection study carried out at the Max Planck Institute (MPI) of Human Cognitive and Brain Sciences in Leipzig, Germany. Participants were recruited through advertisements and were screened for past and present psychiatric and neurological conditions before participation. All participants fulfilled the MRI safety requirements for the MPI and provided written informed consent prior to any testing. Upon completing the study, all participants were monetarily reimbursed. The Ethics committee of the Faculty of Medicine of the University of Leipzig approved this study.

2.2. Behavioral methods

We used the 4-item “Mind-wandering: Deliberate” (MW-D) scale and the 4-item “Mind-wandering: Spontaneous” (MW-S) scale to index trait-level tendencies to deliberate and spontaneous mind-wandering (Carriere et al., 2013). Given that our sample consisted of German-

speaking participants, the MW-D and MW-S questionnaires were translated into German by a professional translator. The MW-D includes items that are related to deliberate/intentional mind-wandering, such as: “I allow my thoughts to wander on purpose,” whereas the MW-S includes items that are related to spontaneous/unintentional mind-wandering, such as: “I find my thoughts wandering spontaneously.” Both scales are scored using a five-point Likert scale ranging from 1 (almost never) to 5 (very often). Both scales showed good internal consistency (Cronbach’s alpha; MW-D: $\alpha=.74$; MW-S: $\alpha=.76$) and were moderately correlated ($r=0.41$, $p < 0.01$).

2.3. MRI data

MRI data were recorded on a 3T Siemens Magnetom Verio Scanner and comprised four resting-state functional magnetic resonance imaging (rs-fMRI) scans and a high-resolution structural image: The rs-fMRI data were acquired using a blood-oxygen-level dependent (BOLD) multiband echo-planar imaging (EPI) sequence with the following parameters: TR=1400 ms, TE=39.4 ms, flip angle=69°, multiband acceleration factor=4, voxel size=2.3 mm isotropic, 64 slices, 657 volumes, duration=15.30 min). In total, 62 min of rs-fMRI data were included for each participant. In order to correct for magnetic field inhomogeneities, field maps for each resting state scan were additionally acquired (TR=0.68 s, TE1=5.19 ms, TE2=7.65 ms, flip angle=60°, voxel size=2.3 mm isotropic, 64 slices). The high-resolution structural image was recorded utilizing a MP2RAGE sequence (Marques et al., 2010; TR=5000 ms, TE=2.92 ms, TI₁=700 ms, TI₂=2500 ms, flip angle₁=4°, flip angle₂=5°, voxel size=1.0 mm isotropic, duration=8.22 min).

To evaluate the functional connectivity results of the current analyses, rs-fMRI data (N=92) from a publicly available independent dataset — enhanced Nathan Kline Institute-Rockland Sample (NKI-RS; Noonan et al., 2012) — were additionally analyzed. These data were acquired on a 3 T Siemens Trio Scanner including an rs-fMRI scan recorded with a BOLD-weighted multiband EPI sequence (TR=645 ms, TE=30 ms, flip angle=60°, multiband acceleration factor=4, voxel size=3 mm isotropic, 40 slices, 900 volumes, duration=10 min). In addition, a high-resolution structural T1-weighted image was acquired using a MP2RAGE sequence (TR=1900 ms, TE=2.52 ms, flip angle=9°, voxel size=1.0 mm isotropic).

2.4. Preprocessing

The preprocessing workflow (which is available online for reproducibility¹) was implemented using Nipype (Gorgolewski et al., 2011), encompassing software from FreeSurfer (Dale et al., 1999; Fischl et al., 1999), FSL (Jenkinson et al., 2012), AFNI (Cox, 1996), ANTs (Avants et al., 2011), CBS Tools (Bazin et al., 2014), and Nitime (Rokem et al., 2009).

2.4.1. Structural MRI

The background of the MP2RAGE images was masked utilizing CBS Tools. Diffeomorphic nonlinear registration (ANTs SyN) was applied to compute a spatial transformation between the individual T1-weighted images and MNI152 standard space. FreeSurfer software (<http://surfer.nmr.mgh.harvard.edu>) was used to generate models of the cortical surface and to model cortical thickness from the T1-weighted images. Previous work has validated FreeSurfer by comparing it with histological analysis (Rosas et al., 2002) and manual measurements (Kuperberg et al., 2003). The processing steps have been described in detail elsewhere (Dale et al., 1999; Fischl et al., 1999; Han et al., 2006). Following surface extraction, sulcal and gyral features across individual

participants were aligned by morphing each participant’s brain to an average spherical representation, which allows for accurate matching of cortical thickness measurement locations among participants while minimizing metric distortion. The entire cortex in each participant was visually inspected and quality-controlled. For whole-brain analysis, thickness data were smoothed on the tessellated surfaces using a 20 mm full-width-at-half-maximum (FWHM) Gaussian kernel prior to statistical analysis. Selecting a surface-based kernel reduces measurement noise but preserves the capacity for anatomical localization, as it respects cortical topological features (Lerch and Evans, 2005).

2.4.2. Functional processing

The following processing steps were applied to the rs-fMRI data: removal of the first five volumes to allow for signal equilibration, motion correction, distortion correction, and coregistration to the individual T1-weighted image. This was followed by (a) removal of 6 motion regressors and first derivatives, motion, and signal-intensity outliers (Nipype rapidart interface) as well as linear and quadratic trends in a general linear model (GLM); (b) elimination of 6 principal components most indicative of physiological noise (aCompCor; Behzadi et al., 2007), together with the initial regressors in a second GLM. Bandpass temporal filtering (0.01–0.1 Hz), mean centering, and variance normalization of the denoised time series were implemented using Nitime. Finally, the time series were projected to MNI152 standard space (2 mm isotropic) using the transformation obtained from the structural preprocessing. We did not perform global-signal regression on these data as this has been shown to introduce artefacts within functional-connectivity data (Saad et al., 2012, 2013).

Preprocessing² of the NKI-RS data was almost identical; however, distortion correction could not be performed because no field maps were available. Denoising was implemented in one regression step, including the Friston 24-parameter-model for motion correction (Friston et al., 1996), five principal components (aCompCor), signal-intensity outliers, as well as linear and quadratic trends.

2.4.3. Regions of interest definition

To best capture relevant aspects of the FPN, we selected regions-of-interest (ROIs) based on peak coordinates from the multiple-demand network reported by Duncan (2010). We included seeds in the left and right inferior frontal sulcus (IFS, MNI ± 41,23,29), intraparietal sulcus (IPS, ± 37,-56,41), and pre-supplementary motor area (pre-SMA, 0,18,50). Time series were extracted and averaged from all voxels within a 3 mm radius spherical ROI centered on each coordinate. The averaged time series from each seed ROI were then correlated with every other voxel in the brain using AFNI’s 3dfim+ command. The resultant correlation maps were Fisher’s r-to-z converted and smoothed with a Gaussian kernel of 6 mm FWHM. This procedure was applied to all four resting-state scans independently, and the resultant maps were then averaged.

2.5. Statistical analysis

2.5.1. Cortical thickness analysis

SurfStat (<http://www.math.mcgill.ca/keith/surfstat>) for Matlab (The Mathworks, Natick, MA) (Worsley et al., 2009) was used to conduct surface-wide cortical-thickness analysis including 121 participants (two outliers, defined by mean cortical thickness > 2.5 SD, were excluded). Within a GLM-framework, normalized scores of spontaneous and deliberate mind-wandering, age, sex, and mean cortical thickness were entered simultaneously into the model. Findings from our surface-based analysis were controlled using

¹ https://github.com/NeuroanatomyAndConnectivity/pipelines/blob/master/src/lsd_lemon/lsd_resting.py.

² https://github.com/NeuroanatomyAndConnectivity/nki_nilearn/blob/master/preprocessing_pipeline.py.

random field theory for non-isotropic images (cluster inclusion threshold: $p=0.025$). This controlled the chance of reporting a family wise error (FWE) to $p < 0.05$, one-tailed.

2.5.2. Resting-state functional connectivity

Group-level multiple-regression analyses were conducted using FSLs FEAT ordinary-least-squares estimation. Standardized scores of self-reported tendencies to spontaneously and deliberately mind-wander were included as predictors, whereas sex, age, and in-scanner motion (mean framewise displacement; Power et al., 2012) were treated as covariates of no interest. For each of the five seeds, a separate model was analyzed, treating the respective connectivity maps as dependent variable. The obtained spatial maps were then thresholded at $z > 2.3$ and $p < 0.005$ (using FSLs easythresh) to account for the number of voxels, seed regions, as well as the positive and negative contrasts ($p < 0.05$ FWE/10= $p < 0.005$). This resulted in thresholded z-stat maps for each seed, reflecting the connectivity patterns associated with the two types of mind-wandering. We have included all of the unthresholded spatial maps produced in these analyses in a publicly available collection at Neurovault at the following URL: neurovault.org/collections/CZZUMFUUY.

3. Results

3.1. Cortical thickness

We first characterized the regions whose cortical thickness varied with the self-reported rates of deliberate and spontaneous mind-wandering (see Fig. 1). A cluster in the right prefrontal cortex (presented in green) had greater cortical thickness for participants who reported higher rates of deliberate mind-wandering. This extended from the dorsal regions of the medial prefrontal cortex to the inferior frontal sulcus. On the other hand, a cluster extending from the left intraparietal sulcus to posterior regions of the temporal lobe (presented in yellow) was thinner for individuals who reported higher rates of

spontaneous mind-wandering. We also observed a double dissociation in terms of thickness in the retrosplenial cortex/lingual gyrus, with higher rates of deliberate mind-wandering being associated with cortical thinning in the right hemisphere (presented in blue), and higher rates of spontaneous mind-wandering being associated with cortical thickening in the left hemisphere (presented in red). The scatterplots present the linear relation between cortical thickness in each cluster, and the inter-individual reports on the respective dimension of mind-wandering.

3.2. Functional connectivity

Having identified the grey-matter structural differences that relate to self-reported rates of deliberate and spontaneous mind-wandering, we next explored the functional architecture associated with these two types of mind-wandering. To understand whether the intentionality in mind-wandering may reflect a differential role of control, we focused on regions which are known to play a domain-general role in controlled cognitive states (e.g. Fedorenko et al., 2013). In particular, we focused on three regions: (a) the inferior frontal sulcus (IFS), (b) the intraparietal sulcus (IPS), and (c) the pre-supplementary motor area (pre-SMA), each of which is reliably activated when cognition needs to be organized with respect to a specific goal such as solving novel problems (cf. Fedorenko et al., 2013). The seeding from the pre-SMA and right IFS yielded no significant results and will not be discussed further (however, their unthresholded maps are available online at Neurovault; see above).

Seeding from the left IFS revealed a distributed network of regions that were more strongly coupled with higher rates of deliberate mind-wandering (see Fig. 2). These regions are presented in green and include the right rostral prefrontal cortex, bilateral regions in the anterior temporal lobe and in the anterior insula, and a cluster extending from the left posterior superior temporal gyrus to the angular gyrus. Seeding from the left IPS revealed a cluster of greater functional connectivity (presented in red), which included the superior

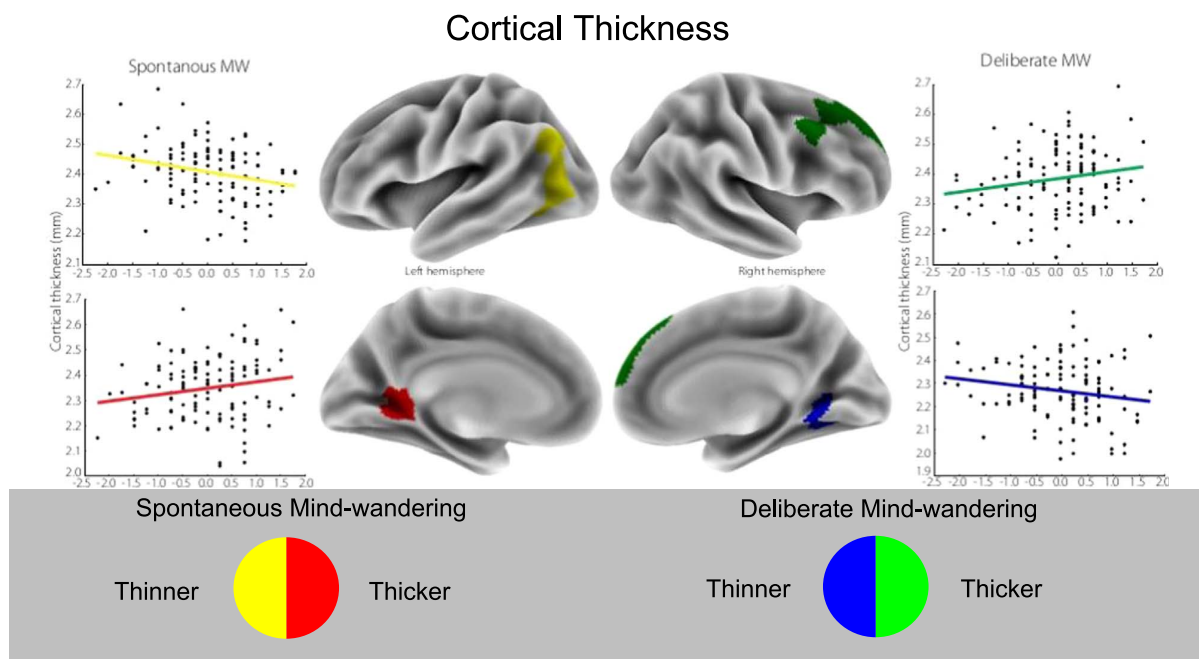


Fig. 1. The results of a whole-brain search of the thickness of grey matter in relation to the levels of intentionality in mind-wandering. Thicker cortical grey matter in a region of dorsal medial/dorsolateral prefrontal cortex was associated with more deliberation in mind-wandering. Thinner cortical grey matter in left parietal and posterior temporal cortex was associated with more spontaneous mind-wandering. In addition, we observed a dissociation in the thickness of the retrosplenial cortex/lingual gyrus with thinner cortex in the right hemisphere associated with less deliberation and greater thickness in the left hemisphere associated with more spontaneous mind-wandering. Spatial maps are thresholded at $p < .01$ FWE corrected. The scatterplots reflect the inter-personal correlation between cortical thickness and the two different types of mind-wandering.

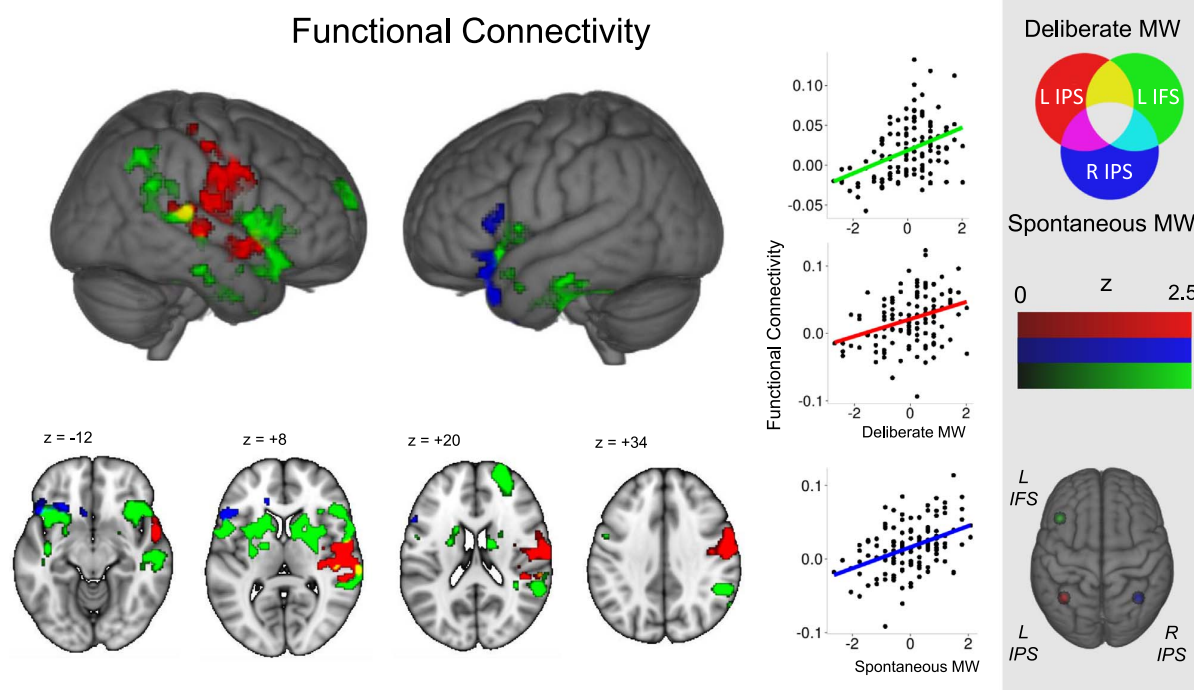


Fig. 2. Functional connectivity associated with deliberate and spontaneous mind-wandering. Cluster-corrected functional-connectivity maps of seeds in left inferior frontal (green) and intraparietal sulcus (red) as positively predicted by deliberate mind-wandering. The regions in blue represent the cluster corrected maps of the right intraparietal sulcus as positively predicted by spontaneous mind-wandering. The corresponding seed-regions are described in the subpanel. Spatial maps have been thresholded at $z > 2.3$ and corrected for multiple comparisons at $p < 0.005$ (FWE). The scatterplots reflect the inter-personal correlation between functional connectivity and different types of mind-wandering, whereas the x-axis reflects an individual's score on the respective questionnaire and the y-axis describes the correlation between the seed region and the cluster highlighted in the figure.

Table 1
Regions significantly related to deliberate and spontaneous mind-wandering.

Seed	MNI coords	Mind-wandering dimension	Cluster centre of gravity	Cluster size (voxels)	Regions	p-Value
lIFS	-41,23,29	MW-D	-38,-1.13,-10.7	3121	aITG/MTG/TP/PP/aIC/OFC/IFG/Pre CG	2.79×10^{-5}
		MW-S	40.3,-1.1,2.4	5524	aITG/pITG MTG/STG/TP/AG/SMG/aIC/OC/IFG/MFG/FP/OFC	5.96×10^{-8}
lIPS	-37,-56,41	MW-D	55.5,-12.3,17.4	2762	TP/STG/Heschl's Gyrus/OC/SMG/Pre/post CG/aIPS	2.62×10^{-6}
rIPS	37,-56,41	MW-S	-35.3,20.5,-14.1	1394	IFG/OFC/TP/subgenual ACC	1.94×10^{-4}

Note. Spatial maps have been thresholded at $z > 2.3$ and corrected for multiple comparisons at $p < 0.005$ (FWE).

Acronyms: MW-D/MW-S=deliberate/spontaneous mind-wandering, (a)ITG=(anterior) inferior temporal gyrus, (p)ITG=(posterior) inferior temporal gyrus, MTG=middle temporal gyrus, AG=angular gyrus, PP=planum polare, (a)IC=(anterior) insular cortex TP=temporal pole, (p)STG=(posterior) superior temporal gyrus, OC=opercular cortex, MFG=middle frontal gyrus, FP=frontal pole, SMG=supramarginal gyrus, Pre/Post CG=pre/post central gyrus, (a)IPS=(anterior) intraparietal sulcus, IFG=inferior frontal gyrus, OFC=orbito frontal cortex, ACC=anterior cingulate cortex.

temporal gyrus, and which extended into the anterior IPS for participants who reported higher rates of deliberate mind-wandering. Finally, seeding from the right intraparietal sulcus revealed a cluster (presented in blue) in ventral regions of the left inferior frontal gyrus and the temporal pole that exhibited greater functional connectivity for participants who reported higher rates of spontaneous mind-wandering. The scatterplots present the between-subject correlation for both types of mind-wandering, as well as the functional connectivity within each spatial map. A complete description of the regions produced through the functional-connectivity analyses is presented in Table 1.

3.3. Relation to large-scale networks

Having identified patterns of structural and functional cortical organization that are associated with self-reported rates of spontaneous and deliberate mind-wandering, we next examined how these patterns related to the spatial distribution of well-described large-scale networks including the DMN and other elements of higher cognition (Yeo

et al., 2011). We compared the spatial maps of both the cortical-thickness and functional-connectivity correlates of deliberate mind-wandering with maps of the DMN and FPN as defined by the publicly available maps produced by Yeo et al. (2011) to determine whether our data supported the hypothesis that deliberate mind-wandering is associated with integration between these two systems. For individuals with higher rates of deliberate mind-wandering, there was overlap with both networks for the functional-connectivity and cortical-thickness maps (see Fig. 3: overlap with the DMN is shown in cyan, whereas overlap with the executive network is shown in yellow). Functional-connectivity analyses from the left IFS identified two regions at the intersection of the FPN and DMN: the right supramarginal gyrus and the right dorsolateral prefrontal cortex. It also revealed regions that are exclusively in the DMN: The right angular gyrus and the ventral anterior inferior frontal gyrus. Cortical-thickness analyses also implicated adjacent regions in the DMN and FPN: The pre-SMA, the dorsomedial prefrontal cortex, and the right IFS. Importantly, both structural and functional-connectivity results implicated regions that

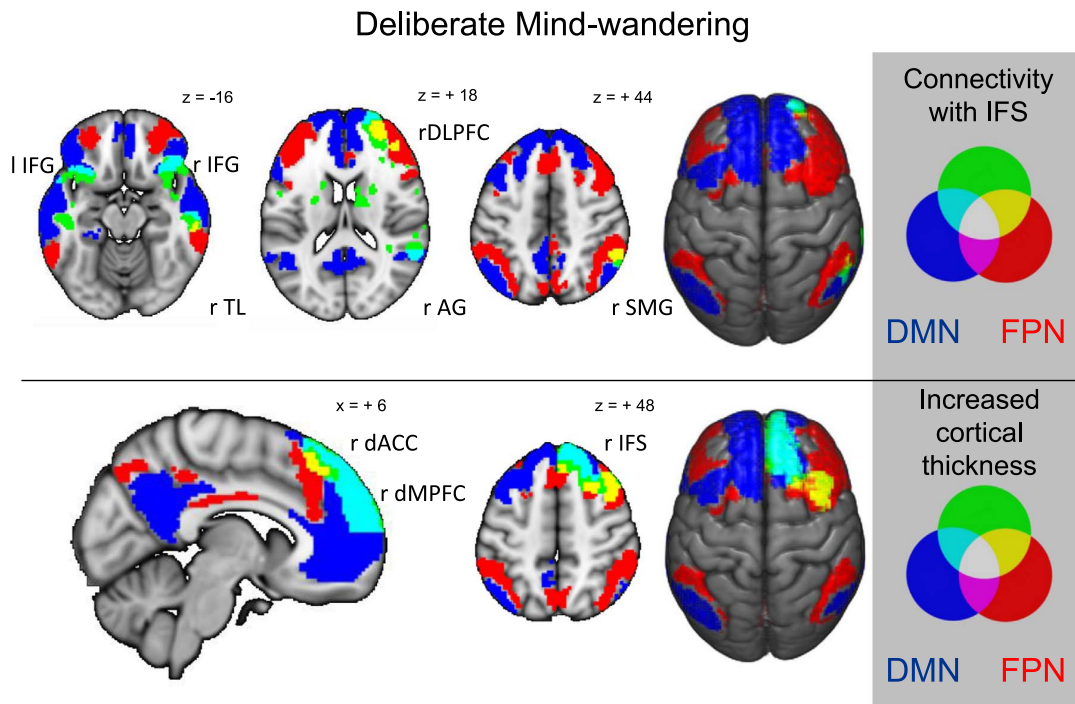


Fig. 3. Functional connectivity and cortical thickness clusters related to deliberate mind-wandering overlap with regions of the default-mode and executive network. This figure shows the spatial overlap between the default-mode network (DMN, blue), as well as the fronto-parietal executive network (FPN, red; using the spatial maps made available by Yeo et al. (2011)) and the functional connectivity results of the left inferior frontal sulcus (IFS, upper panel) and the whole brain cortical thickness analyses (lower panel) associated with deliberate mind-wandering. To maximize the visibility of spatial overlap, all maps are fully saturated.

bridge the DMN and FPN as being important in individuals who reported higher rates of deliberate mind-wandering. The observation that higher deliberate mind-wandering was associated clusters in both the DMN and FPN suggests that the process of mind-wandering in a deliberate manner depends, in part, on the integration of the executive control and default mode networks as predicted by contemporary accounts of this experience (see Smallwood et al., 2011; Smallwood, 2013; Smallwood and Schooler, 2015).

In contrast, our results suggest that a different pattern of cortical organization may underlie reports of spontaneous mind-wandering: In particular, participants who reported higher rates of spontaneous mind-wandering tended to have cortical thinning in left angular gyrus within the DMN, extending to regions in the IPS implicated in executive control (Fig. 4). Cortical thinning in these areas could make it more difficult for functional integration between these two large-scale networks. Instead of reflecting integration between the DMN and the

executive network, our functional-connectivity results implicated greater involvement of the limbic network in spontaneous mind-wandering (see Fig. 5). Regions within the DMN included the left retrosplenial cortex/lingual gyrus and the left dorsal inferior frontal gyrus, whereas limbic regions included the ventral anterior temporal lobe and inferior frontal gyrus (both in the left hemisphere). Underlining the difference between the patterns of cortical organization associated with spontaneous and deliberate mind-wandering, the latter was associated with thinner retrosplenial cortex/lingual gyrus in the left hemisphere.

3.4. Commonalities in spontaneous and deliberate mind-wandering

Our final analysis considered regions that were implicated in both spontaneous and deliberate mind-wandering. We identified an overlap in the connectivity of the left IFS (associated with higher reports of deliberate mind-wandering) and the right IPS (associated with higher

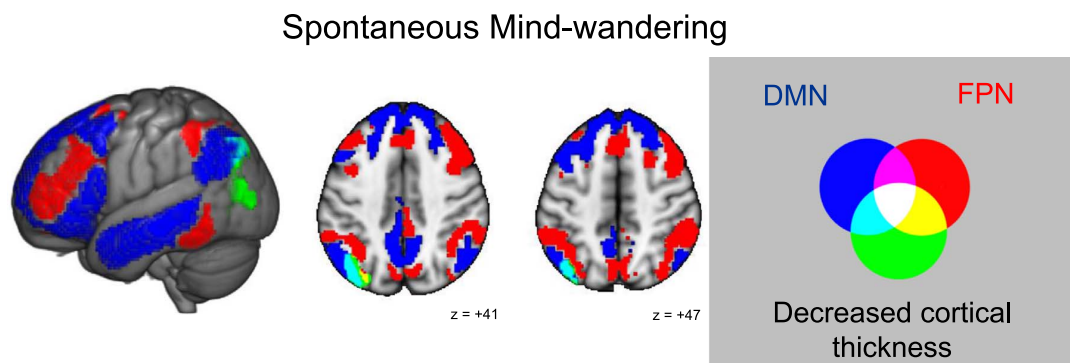


Fig. 4. Cortical thinning associated with spontaneous mind-wandering overlaps with parietal regions of the default-mode and executive network. This figure illustrates the spatial overlap between the cortical thickness results related to spontaneous mind-wandering and two large-scale networks: the default-mode network (DMN, blue) and fronto-parietal network (FPN, red). To maximize the visibility of spatial overlap, all maps are fully saturated.

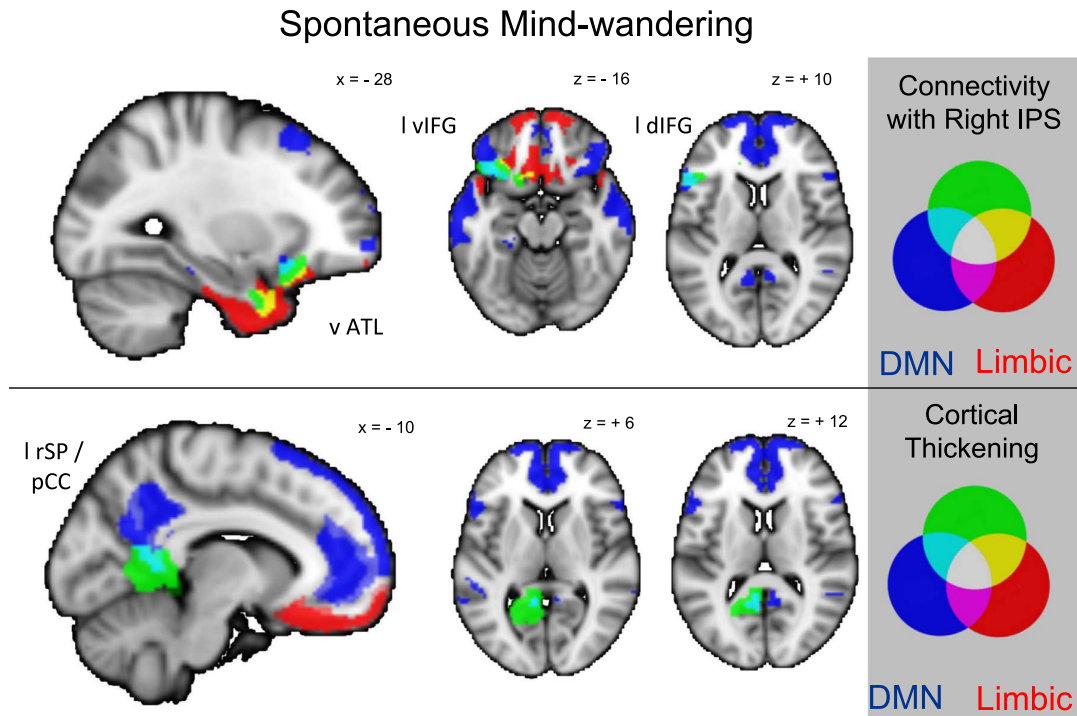


Fig. 5. Functional connectivity and cortical thickness clusters related to spontaneous mind-wandering overlap with regions of the default mode and limbic network. This figure displays the spatial overlap between the default-mode network (DMN, blue) as well as limbic (red) network, and the functional connectivity results of the right intraparietal sulcus (IPS, upper panel). The whole brain cortical-thickness analyses associated with spontaneous mind-wandering is presented in the lower panel. To maximize the visibility of spatial overlap, all maps are fully saturated.

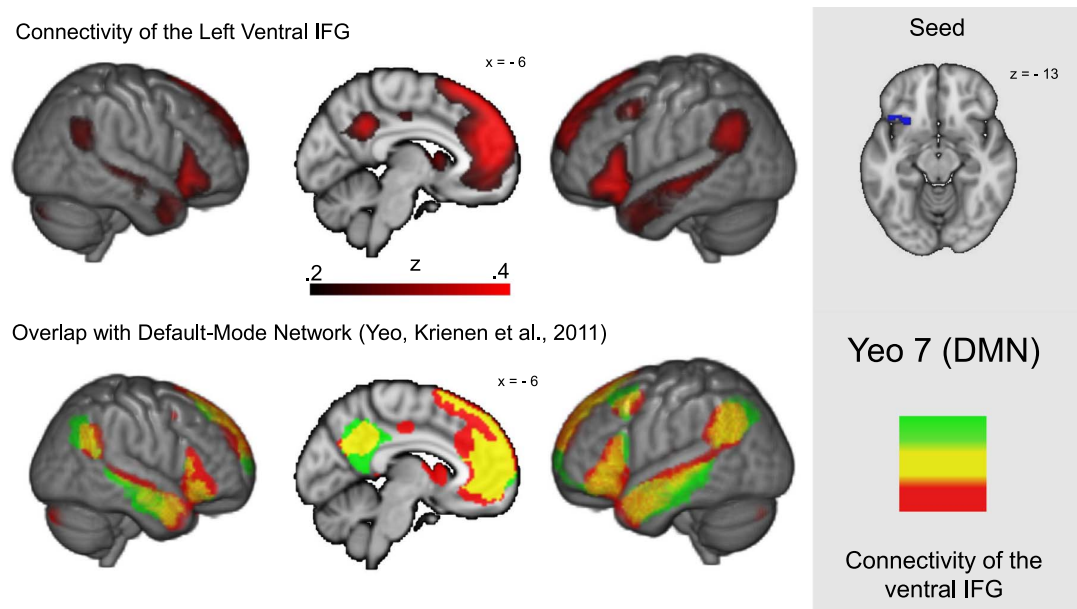


Fig. 6. Region-of-interest analysis of the left ventral IFG investigating its functional-connectivity profile in an independent dataset. The upper right panel illustrates the region of interest derived by the former connectivity analysis. The upper left panel shows the group functional-connectivity profile of the left ventral Inferior Frontal Gyrus (IFG), which demonstrates extensive spatial overlap with the default-mode network defined by Yeo and colleagues (lower left panel). The seed that was used to generate the connectivity maps is presented in the subpanel. To maximize the visibility of spatial overlap, all maps are fully saturated.

reports of spontaneous mind-wandering) in a region of left ventral inferior frontal gyrus. To examine this region, we seeded it in an independent dataset (NKI-RS; see methods), revealing a network that engaged the medial prefrontal cortex, the posterior cingulate cortex, the angular gyrus, and the anterior temporal lobe (see Fig. 6).

Comparison of this network with the DMN, as described by Yeo et al. (2011), indicated a high degree of overlap. This network reflects the functional connectivity of a region that was commonly connected to aspects of the FPN for both spontaneous and deliberate mind-wandering. Thus, left ventral inferior frontal gyrus may be important to DMN/

executive network interactions during mind-wandering regardless of the level of intentionality.

4. Discussion

In the current study, we sought to determine whether the integration between the DMN and executive network is related to inter-individual trait differences in rates of deliberate and spontaneous mind-wandering. Using a combination of different imaging modalities, we demonstrated that participants who reported higher rates of deliberate mind-wandering tended to show a pattern of heightened integration between the DMN and regions of the FPN. This pattern was observed primarily in prefrontal regions, including the medial prefrontal cortex and the anterior cingulate cortex, as well as in regions of the rostral and dorsolateral prefrontal cortex. By contrast, participants who reported higher rates of spontaneous mind-wandering showed cortical thinning in regions of the right parietal cortex, which encompassed adjacent regions of both the DMN and the FPN. Critically, these results support the hypothesis that more effective communication between regions of the DMN and the FPN is associated with mind-wandering that is more aligned with an individual's intentions.

Taken together, the findings reported here provide both structural and functional evidence to support the hypothesis that executive control is important in constraining cognition such that inner experiences unfold in a more deliberate fashion (see also Christoff et al. (2016) and Seli et al. (2016d)). Importantly, this perspective aligns well with research that has examined “event planning” (Baird et al., 2011; Smallwood et al., 2009): a cognitive process that is commonly reported during the mind-wandering state, and one that has been shown to rely on executive-control processes. Indeed, recent studies have provided ample evidence to suggest that the DMN and FPN are coupled when people plan the future (Fox et al., 2015; Gerlach et al., 2011, 2014; Spreng et al., 2010). More generally speaking, our perspective also aligns well with an emerging literature from the neuroimaging of task states, which highlights interactions between the DMN and FPN in tasks that depend on the retrieval of information from memory, including working-memory tasks (Konishi et al., 2015; Vatansever et al., 2015), demanding semantic tasks (Krieger-Redwood et al., 2016) and tasks assessing creativity (Beaty et al., 2015; Benedek et al., 2016). Based on these findings, we suggest that coupling between the DMN and FPN is important in allowing cognition to proceed along specific goal-relevant lines, and that, during the mind-wandering state, this capacity underlies the ability to deliberately guide a self-generated train of thought (Smallwood, 2013; Seli et al., 2016d).

Intriguingly, our study highlighted the insula as one region that was connected to the left IFS for individuals who reported higher rates of deliberate mind-wandering (see Fig. 2). This region, along with regions of cingulate cortex, makes up the so-called the “saliency network” (Seeley et al., 2007), which is thought to play an important role in controlling the interactions between the DMN and the FPN (Bonnelle et al., 2012; Goulden et al., 2014; Sridharan et al., 2008). Based on these findings, we hypothesize that the saliency network could be important in regulating mind-wandering so as to ensure that it proceeds in a deliberate manner: a prediction that is consistent with our prior research demonstrating that the anterior cingulate cortex helped to regulate mind-wandering across low- and high-demanding task conditions (Bernhardt et al., 2014).

Our data also provide important, albeit indirect, support for the hypothesis that limbic structures – such as the hippocampus and the medial anterior temporal lobe – are important in the initiation of mind-wandering (cf. Buckner, 2010; Smallwood, 2013). The hypothesis that the hippocampus is important in the initiation of the mind-wandering state was recently supported by an experience-sampling study that examined mind-wandering in experienced meditators (Ellamil et al., 2016). Here, the authors found that the hippocampus was activated relatively early on during the mind-wandering state.

Consistent with this finding, our data indicate that spontaneous, but not deliberate, mind-wandering is associated with increased cortical thickness in the retrosplenial cortex: a region that is hypothesized to be important for the integration of information from the hippocampus, with representations from other aspects of cortex, such as the parietal lobe (Vann et al., 2009). Importantly, these results may indicate that the spontaneous onset of mind-wandering occurs when activity in the hippocampus is integrated into an ongoing train of thought via the retrosplenial cortex. A role for limbic structures in the spontaneous initiation of mind-wandering episodes is also supported by our observation that reports of spontaneous mind-wandering experiences (i.e., mind-wandering that lacks intention) showed heightened coupling between the right IPS and a region of the medial temporal lobe (see Fig. 5). Although our data are consistent with the hypothesis that the onset of self-generated thought during mind-wandering may depend on spontaneous changes that take place in limbic structures, our analysis occurred at the trait level, and hence, firm conclusions on this issue require a study in which the neural signature of deliberate and spontaneous mind-wandering experiences are assessed online. Thus, we recommend that this hypothesis is treated with caution until it is tested in a study that examines the neural changes that occur when mind-wandering is deliberate or spontaneous.

There are a number of limitations that should be borne in mind while considering the results of the current study. First, we applied cluster correction to control for multiple comparisons in both our cortical thickness and functional connectivity analyses. Although our sample is relatively large for a study of this type (which makes it unlikely that our results are spurious), Eklund et al. (2016) have recently shown that alpha estimates based on cluster correction are subject to error, and as such, our cluster-corrected results should be interpreted with caution. Second, although our analyses focused on identifying the neural correlates of deliberate and spontaneous mind-wandering, we did not explicitly contrast these two types of mind-wandering. It is therefore important to interpret our findings in terms of describing the neurocognitive correlates of different types of mind-wandering, rather than in terms of highlighting the differences between the two types of mind-wandering. Third, our study examined differences in the intentionality of mind-wandering at the trait-level. It is therefore important to note that these findings illustrate differences across people who differ in terms of the relative levels of deliberation that they tend to experience during mind-wandering. Assessing the state-related changes in neural processing between deliberate and spontaneous mind-wandering would require a study in which participants are presented with online (i.e., in the moment) “thought probes,” which would allow researchers to identify periods of time during which participants are engaged in deliberate and spontaneous mind-wandering (ideally, such a study would take place across multiple sessions, as this would allow trait-level influences to be most clearly dissociated from state-level influences on deliberate and spontaneous mind-wandering). Fourth, our seed-based connectivity analysis was exclusively focused on regions in the frontal parietal cortex, as these regions have been hypothesized to play an important role in dictating the intentionality associated with a given episode of mind-wandering (Seli et al., 2016b; Smallwood and Schooler, 2015). It is, however, important to note that other regions may likewise play an important role in dictating the intentionality of mind wandering. For example, theoretical accounts have implicated the medial temporal lobe as being important in initiating spontaneous elements of mind-wandering (Smallwood, 2013). Thus, exploring the relationship between the medial temporal lobe and the intentionality of mind wandering will an important area for future research.

In conclusion, the current results offer a neurocognitive explanation for why mind-wandering has a complex, and often confusing, relationship with executive control. Using MRI descriptions of cortical structure and functional connectivity, we showed that the relationship between the DMN and the executive network varies across individuals

as a function of the frequency at which they report deliberate and spontaneous mind-wandering. Given that executive control is known to aid in the regulation of cognition (e.g. Duncan, 2010), the integration between the DMN and FPN could suggest that deliberate mind-wandering might be a further example of the domain-general nature of cognitive control. Our study also underscores the general value of exploring different features of the mental content that emerge during the mind-wandering state (Smallwood and Andrews-Hanna, 2013; Smallwood and Schooler, 2015). Here, we focused on a single dimension of experience: namely, intentionality. However, it is possible that other experiential features of mind-wandering content could emerge from distinct neural mechanisms. Thus, we encourage researchers to examine the neural signatures of multiple different aspects of experience (e.g. Smallwood et al., 2016), as such investigations will likely shed important light on the neural basis that underlies the different types of experiences that can occur during the mind-wandering state.

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Lebenslauf

Mein Lebenslauf wird aus datenschutzrechtlichen Gründen in der elektronischen Version meiner Arbeit nicht veröffentlicht.

Publikationsliste

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