States of Mind: Characterizing the Neural Bases of Focus and Mind-wandering through Dynamic Functional Connectivity

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Abstract

■ During tasks that require continuous engagement, the mind alternates between mental states of focused attention and mind-wandering. Existing research has assessed the functional connectivity of intrinsic brain networks underlying the experience and training of these mental states using "static" approaches that assess connectivity across an entire task. To disentangle the different functional connectivity between brain regions that occur as the mind fluctuates between discrete brain states, we employed a dynamic functional connectivity approach that characterized brain activity using a sliding window. This approach identified distinct states of functional connectivity between regions of the executive control, salience, and default networks during a task requiring sustained attention to the sensations of breathing. The frequency of these distinct brain states demonstrated opposing correlations with dispositional mindfulness, suggesting a correspondence to the mental states of focused attention and mind-wandering. We then determined that an intervention emphasizing the cultivation of mindfulness increased the frequency of the state that had been associated with a greater propensity for focused attention, especially for those who improved most in dispositional mindfulness. These findings provide supporting evidence that mind-wandering involves the corecruitment of brain regions within the executive and default networks. More generally, this work illustrates how emerging neuroimaging methods may allow for the characterization of discrete brain states based on patterns of functional connectivity even when external indications of these states are difficult or impossible to measure. ■

INTRODUCTION

Both subjective experience and empirical research clearly indicate that at least two mental states intermittently occur during tasks requiring continuous attention: focused attention and mind-wandering. Considerable interest exists in the cognitive and neural characterizations of these states, including whether the frequency of these states is alterable through training (Mrazek, Franklin, Phillips, Baird, & Schooler, 2013; Hasenkamp, Wilson-Mendenhall, Duncan, & Barsalou, 2012; Slagter, Davidson, & Lutz, 2011; Voss et al., 2010; Zeidan, Johnson, Diamond, David, & Goolkasian, 2010; Lutz et al., 2009; Tamm et al., 2009; Tang & Posner, 2009). Yet, in part because of the challenge of knowing precisely when these states occur, many questions remain regarding the neural basis of both focused attention and mind-wandering.

The role of executive functions in mind-wandering remains an issue of particular debate (Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015; Smallwood & Schooler, 2006, 2015; Smallwood, 2010, 2013; Kane & McVay, 2012; Baird, Smallwood, & Schooler, 2011; McVay & Kane, 2009, 2010; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009). Mind-wandering is a ubiquitous mental state characterized by a shift of attention away from a task toward task-unrelated concerns. This state is associated with impaired performance across virtually any task requiring continuous attention (Mooneyham & Schooler, 2013; Mrazek et al., 2013). Individuals who mind-wander more often also tend to have lower levels of executive control (McVay & Kane, 2009; Kane et al., 2007), and mind-wandering appears to play a mediating role in the relationship between working memory capacity and task performance (Kane & McVay, 2012). These findings have been interpreted as evidence that mind-wandering represents a failure of executive control over one's thoughts, resulting in the intrusion of task-unrelated thoughts within task settings. The idea that processes associated with executive control and mind-wandering are largely oppositional is loosely supported by evidence that the default network (DN)—a set of brain regions whose activity is strongly associated with the occurrence of mind-wandering and spontaneous cognition (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Christoff et al., 2009; Buckner, Andrews-Hanna, & Schacter, 2008)—shows anticorrelated activity with regions of the executive network both at rest (Fox et al., 2005) and during task settings (Hellyer et al., 2014; Wen, Liu, Yao, & Ding, 2013; Gao & Lin, 2012; Brewer et al., 2011).[1]

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However, the role of executive control processes during mind-wandering remains poorly understood. Mind-wandering during a task is associated with increased activation of both default and executive regions (Fox et al., 2015; Christoff et al., 2009; Mason et al., 2007). This evidence weighs in favor of a "corecruitment" mind-wandering hypothesis in which executive control processes are employed in the service of maintaining mind-wandering episodes (Schooler et al., 2011; Christoff et al., 2009; Smallwood & Schooler, 2006). However, not all studies have shown this pattern of executive and default activation during mind-wandering (Hasenkamp et al., 2012). Furthermore, brain regions that are active during a particular task or mental state may work either cooperatively or antagonistically. Given that the functional connectivity (FC) between executive network (EN) and DN during mind-wandering has not yet been directly examined, the role of these networks in supporting mind-wandering remains ambiguous.

A major limitation to scientific investigation into states of focus or mind-wandering is knowing when these mental states occur (Franklin, Mooneyham, Baird, & Schooler, 2014; Smallwood, 2013; Franklin, Smallwood, & Schooler, 2011). To date, the most reliable method for determining the occurrence of mind-wandering is thought sampling, where participants are interrupted during a task at unpredictable intervals and asked to report the focus of their attention. Although thought-sampling measures of mind-wandering have provided an invaluable lens into the neural dynamics underlying mind-wandering, they have limitations. First, they cannot determine when an episode of mind-wandering began. Second, they provide inherently limited sampling opportunities, as they may only be employed intermittently throughout a task. Third, although intermittent thought sampling appears to create minimal reactivity in task performance (Mrazek et al., 2013), it nevertheless produces frequent distractions that preclude the investigation of undisturbed fluctuations between cognitive states. For these reasons, converging methods are necessary to further delineate the neural bases of mind-wandering and focused attention.

Dynamic FC as a Tool to Characterize Mental States

Dynamic FC (DFC) analyses provide a promising new method for characterizing the neural basis of mental states such as focused attention and mind-wandering. These approaches characterize discrete states of FC between a set of regions over time during a task or resting state (Allen et al., 2014; Damaraju et al., 2014; Rashid, Damaraju, Pearlson, & Calhoun, 2014). These "chronnectomic" approaches reveal that FC relationships between brain regions and networks fluctuate dynamically over time, likely signifying changes in cognitive states (Calhoun, Miller, Pearlson, & Adalı, 2014; Hutchison et al., 2013). State characterization with DFC analyses is accomplished using data-driven clustering algorithms to identify the number of states that are intrinsically present in the data and to label individual data points according to their state categorization (for a review of the approach, see Calhoun et al., 2014). This allows the number of states to be determined without introducing theoretical biases. The occurrence of states can also be explored without the need for subject responding, providing a nonreactive tool for assessing fluctuations in cognitive states.

DFC approaches have been applied to between-group comparisons, where they have successfully revealed differences in both the frequency of discrete states and the pattern of FC of these states in both clinical and healthy samples (Allen et al., 2014; Damaraju et al., 2014; Rashid et al., 2014). DFC approaches have also been employed in within-participant designs to explain variations in FC during different task types (Jia, Hu, & Deshpande, 2014) and even predict trial-by-trial variations in performance (Sadaghiani, Poline, Kleinschmidt, & D'Esposito, 2015), among other applications. Yet, DFC may also be used to examine longitudinal changes within individuals over time, and this approach may be particularly informative in the context of longitudinal interventions given that alteration of cognition and brain function through training can advance both basic and applied scientific understanding (Slagter et al., 2011). DFC may serve as a valuable tool within longitudinal interventions for discovering changes in brain function that underlie improvements in performance or behavior, thereby elucidating the neural mechanisms by which such outcomes arise.

Mindfulness and mind-wandering represent opposing constructs with respect to sustained attention, and converging research indicates that mindfulness training is an effective tool for enhancing focus and reducing mind-wandering (Zanesco et al., 2016; Mrazek et al., 2013; MacLean et al., 2010). In particular, mindfulness training offered within the context of an intensive lifestyle change intervention leads to dramatic increases in dispositional mindfulness as well as decreases in mind-wandering during laboratory tasks and daily life (Mrazek, Mooneyham, Mrazek, & Schooler, 2016). Accordingly, this research utilized a similar intervention to determine whether the frequency of discrete states of FC that emerge during a mindful breathing task changes as a consequence of training.

Networks Relevant to Sustained Attention

Given that large-scale brain networks have a structural basis and show considerable consistency over time (Bullmore & Sporns, 2009; Fox et al., 2005), rapid changes in cognitive abilities likely arise not in the wholesale rewiring of these intrinsic systems but rather in the modulation of interactions within and between these networks. Recent neuroimaging research has pointed to the activity of at least three key intrinsic networks as being especially important for maintaining focus and avoiding mind-wandering (Mooneyham, Mrazek, Mrazek, & Schooler, 2016): the EN, the salience network (SN), and the DN.

The EN is thought to be involved in the controlled processing of goal-oriented behaviors (Sridharan, Levitin, & Menon, 2008; Seeley et al., 2007; D'Esposito et al., 1995), and it has been shown to be active during sustained attention (Hasenkamp & Barsalou, 2012; Christoff et al., 2009). The SN is involved in the detection and evaluation of motivationally relevant stimuli and is functionally dissociable from the central EN (Menon & Uddin, 2010; Seeley et al., 2007). The DN supports cognition that is independent of immediate sensory input (Konishi, McLaren, Engen, & Smallwood, 2015) and is active during mind-wandering (Hasenkamp & Barsalou, 2012; Christoff et al., 2009; Mason et al., 2007). The DN is also typically deactivated during tasks requiring cognitive control (Greicius, Krasnow, Reiss, & Menon, 2003). Interactions between the EN, SN, and DN have been implicated in shifts of attention to salient information and varying levels of task performance (Wen et al., 2013; Menon & Uddin, 2010; Sridharan et al., 2008).

This Study

In this study, we employed DFC analysis to identify distinct states of FC across the EN, SN, and DN during a task of sustained attention. We then interpreted the cognitive significance of the resulting states through convergence with the existing literature and by relating each state's frequency to levels of dispositional mindfulness. Using a randomized waitlist controlled design, half of these participants then completed a 6-week intensive and multifaceted intervention emphasizing the cultivation of mindfulness (Mrazek et al., 2016). Afterward, we examined the effect of the intervention on levels of dispositional mindfulness and the proportion of time spent in each state during the sustained attention task at posttesting.

METHODS

Thirty-eight college undergraduates (16 men and 22 women; mean age = 20.38 years, SD = 2.28 years) from the University of California, Santa Barbara, were recruited to participate in what was described as an intensive lifestyle change program focused on exercise, nutrition, sleep, mindfulness, compassion, and relationships. The intervention (n = 19) and waitlist control (n = 19) conditions were balanced for age and sex using adaptive covariate randomization. Inclusion criteria were (1) availability for all training and testing sessions, (2) a capacity to engage in physical exercise, and (3) no contraindications for MRI scanning. One participant in the waitlist condition withdrew from the study before the second testing session. After the first 6-week intervention, the remaining 37 participants completed a second round of testing. Participants received financial compensation at the rate of $10/hr for the research testing.

Intervention Program

The training program was modeled after an intervention that has previously been shown to increase dispositional mindfulness and reduce mind-wandering (Mrazek et al., 2016). The intervention convened for 5.5 hr each weekday over a period of 6 weeks. Each day included 150 min of physical exercise, 60 min of formal mindfulness practice, 30 min of structured small group discussion, and 90 min of lecture or discussion on topics related to sleep, nutrition, exercise, mindfulness, compassion, relationships, or well-being. Participants were encouraged to limit alcohol intake to no more than one drink a day, to eat a diet of primarily whole foods, and to consistently sleep at least 8 hr each night. The mindfulness training emphasized focused attention meditation in which attention is directed to a selected aspect of sensory experience (e.g., the physical sensations of breathing or walking; Lutz, Slagter, Dunne, & Davidson, 2008). Class content provided both a conceptual understanding of mindfulness as well as practical strategies for cultivating mindfulness during formal meditation and throughout daily life. With minor exceptions (e.g., temporary illness), all participants attended every session of the intervention. Although the multifaceted structure of this intervention precludes determination of the specific causal factors underlying training-induced improvements, this research aims to characterize the nature and frequency of states of focused attention and mind-wandering and so only requires an intervention that measurably enhances sustained attention.

Measures

Mindful Breathing Scan

At pretesting and posttesting, participants completed a 9-min 42-sec mindful breathing scan. At the onset of the scan, participants were told to attend to and count their breaths (exhalations). The instruction to count and report their breaths was implemented to better ensure task focus during the scan. Because of its continuous and rigidly defined attention requirements, this task represents a test of both sustained attention and cognitive control; it is an ideal task for examining the neural underpinnings of these mental capacities. Participants in the intervention program engaged in approximately an hour of formal mindfulness training each day, and as such, their attentional control skills were expected to improve across the course of the program. By targeting a specifically trained skill within the neuroimaging, we aimed to be able to uncover intervention-induced changes over time within our intervention group that would not be observable within the control group. Mindful breathing is also a popular form of mental training that is practiced by millions of people, and it is therefore a task context with considerable practical relevance.

MRI acquisition. MRIs were obtained using a Siemens (Erlangen, Germany) 3.0-T Magnetom Tim Trio (Syngo MR B17) MRI scanner. Before obtaining the functional data, a high-resolution T1-weighted anatomical scan was acquired for each participant (magnetization prepared rapid gradient echo, repetition time [TR] = 2530 msec, echo time = 3.50 msec, inversion time = 1100 msec, flip angle = 7°, field of view = 256 mm, acquisition voxel size = 1 × 1 × 1 mm). In addition, before obtaining the mindful breathing scan, a resting state scan was obtained; this scan is the subject of independent analyses and therefore is not discussed further in this manuscript. After the resting state scan, the mindful breathing scan was obtained using a T2*-weighted EPI sequence (TR = 1200 msec, echo time = 30 msec, acquisition matrix = 64 × 64, field of view = 192 mm, acquisition voxel size = 3 × 3 × 5 mm, 22 interleaved slices, 480 volumes).

Structural (T1) data processing. Cortical surface reconstruction was performed on T1 scans using FreeSurfer (surfer.nmr.mgh.harvard.edu/). For each participant, nonlinear transformation from T1 to the 2-mm MNI152 template was calculated using Advanced Normalization Tools (stnava.github.io/ANTs/).

Mindful breathing fMRI (EPI) data processing. Functional imaging data preprocessing, described below, was performed according to the procedure first described in Mrazek et al. (2016). The first four volumes of each EPI sequence were removed to eliminate potential effects of scanner instability. Slice timing and motion correction of the EPI images were performed using AFNI, followed by affine co-registration of the mean EPI image and T1 volume using FreeSurfer's BBRegister. Brain, cerebrospinal fluid, and white matter masks were extracted after FreeSurfer parcellation and transformed into EPI space. Coregistered EPI images were then masked using the brain mask. The principal components of physiological noise were estimated and extracted using CompCor (Behzadi, Restom, Liau, & Liu, 2007); motion and intensity outliers in the EPI sequence were also discovered based on intensity and motion parameters using ArtDetect (www.nitrc.org/projects/artifact_detect). All time series were then denoised using a general linear model with the motion parameters, CompCor components, and intensity outliers used as regressors. Finally, resultant time series were smoothed using FreeSurfer with 5-mm FWHM surface and volume kernels; high-pass (0.01 Hz) and low-pass (0.1 Hz) filters were applied using FMRIB Software Library.

ROI selection. Our a priori interest was in the functional relationships between key regions of the EN, SN, and DN. Accordingly, we selected a set of bilateral ROIs drawn from a previous investigation that revealed causal relationships between these three networks across multiple task contexts in both hemispheres (see Table S1 from Sridharan et al., 2008). These ROIs include three medially located regions corresponding to ACC, ventromedial pFC (vmPFC), and posterior cingulate cortex (PCC) and six regions representing bilateral homologues of the fronto-insular cortex (FIC), dorsolateral pFC (dlPFC), and posterior parietal cortex (PPC; Table 1). The medial ROI locations provided by Sridharan et al. (2008) did not originally provide bilateral representation of the anatomical regions being assessed; therefore, for the three medial regions, bilateral seeds were drawn by producing symmetrical ROIs for the left and right hemispheres and then combined to create bilateral versions of the ROIs from Sridharan et al. (2008).

For each of the nine resulting ROIs, 6-mm-radius spheres were drawn around the ROI center coordinate in 2-mm Montreal Neurological Institute (MNI) space, and nonlinear normalization warping from MNI to each participant's native space was performed using Advanced Normalization Tools. Time courses were extracted from each ROI for the pretest and posttest scans.

Dynamic functional connectivity. For each scan, we computed DFC values between each pair of ROIs via a sliding temporal window approach. Each window had a width of 75 TRs (which corresponds to a 90-sec duration). The 75-TR window width was chosen to allow for a large number of individual windows within each scan while providing sufficient data within each window to compute a robust correlation between ROI time courses. The windows progressed in steps of 1 TR, resulting in 401 windows of FC within each individual scan. For each window, Pearson's r was calculated for each pair of ROIs across the window and was Fisher r-to-z transformed, resulting in a 9 × 9 matrix of pairwise FC values for each

Table 1. ROIs

Regions	*Network Affiliation*	*Hemisphere*	*MNI Coordinates*
FIC	SN	Right	37, 25, −4
		Left	−32, 24, −6
ACC	SN	Midline	±4, 30, 30
dlPFC	EN	Right	45, 16, 45
		Left	−45, 16, 45
PPC	EN	Right	54, −50, 50
		Left	−38, −53, 45
vmPFC	DN	Midline	±2, 36, −10
PPC	DN	Midline	±7, −43, 33

The location and network affiliation of the nine ROIs that were extracted for further analysis. Spherical 6-mm ROIs were drawn around the listed MNI coordinates (in millimeters). For midline regions, spherical ROIs were drawn around two separate seed regions symmetrically located about the x axis (midline) and combined to form a joint bilateral seed.

window (the upper triangular values reflect the unique pairwise values and were thus the only values analyzed).

Clustering. To identify common states of FC across the nine ROIs within the data set, all scans from both scanning sessions were concatenated into a single group data set containing all windowed FC matrices. *k*-Means clustering was employed to obtain group centrotypes of DFC. The gap statistic criterion of determining the appropriate number of clusters indicated the largest gap change for a three-cluster solution (for a description of the gap statistic, see Tibshirani, Walther, & Hastie, 2001).

The three group centrotypes were used to classify each individual window of FC within each individual scan based on its similarity to each centrotype. Similarity was calculated based on the total Euclidean distance between the individual FC values within a window's FC matrix and the FC values within each group centrotype. The centrotype that was the smallest total Euclidean distance from a particular window was then associated with that window. Each window from the group data set was therefore labeled as being most similar to one of the three group centrotypes (Figure 1 provides a schematic of the DFC and clustering procedure).

Dispositional Mindfulness

At pretest and posttest, participants reported their dispositional levels of mindfulness using the Mindful Attention and Awareness Scale (MAAS). The order of the administration of this scale and the scanning session were counterbalanced by participants at pretesting, and each participant completed them in the same order at posttesting as they had previously done. This validated scale is the most widely used self-report measure of mindfulness and measures an individual's level of attention to and awareness of what is occurring in the present (e.g., "I find myself preoccupied with the future or the past."). Additional measures not pertinent to the present findings were also recorded, which will be reported in full in a separate article.

Statistical Analyses

Characterizing the FC States through Correlations with Dispositional Mindfulness

The clustering approach characterized each window within a scan as corresponding to one of three functional states, allowing calculations of the proportion of the mindful breathing task that was spent in each state. To

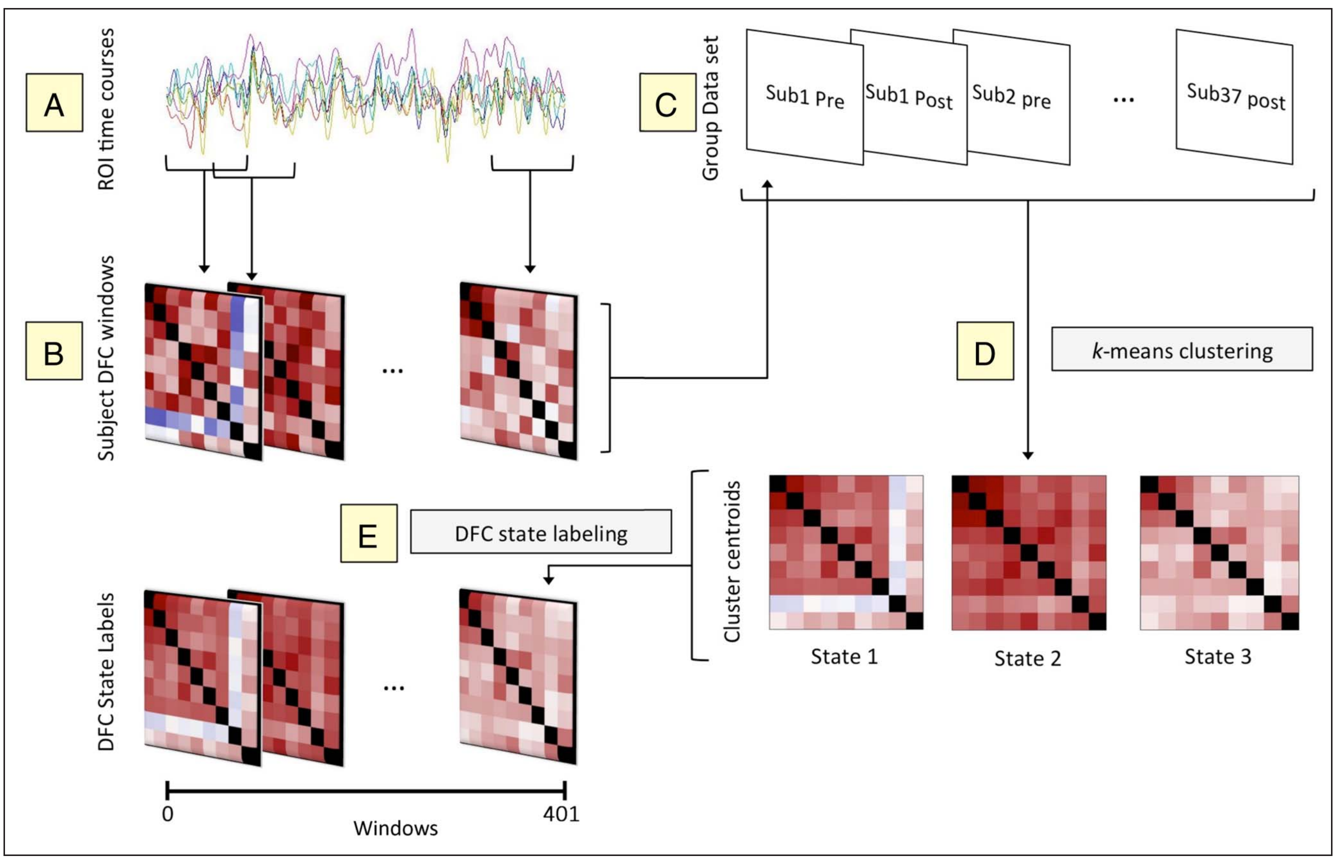

Figure 1. Schematic of the DFC and *k*-means clustering procedure. (A) Time courses for nine ROIs were extracted for each participant and session. (B) A sliding window approach calculated FC within 75 TR segments of the mindful breathing scan; new windows of FC were calculated at each TR step. (C) Pretesting and posttesting scans were concatenated for each participant; a group data set was then created by concatenating all participants. (D) *k*-Means clustering was used to determine three DFC state centrotypes. (E) DFC state centrotypes were used to classify each individual DFC window within the group data set based on Euclidean distance.

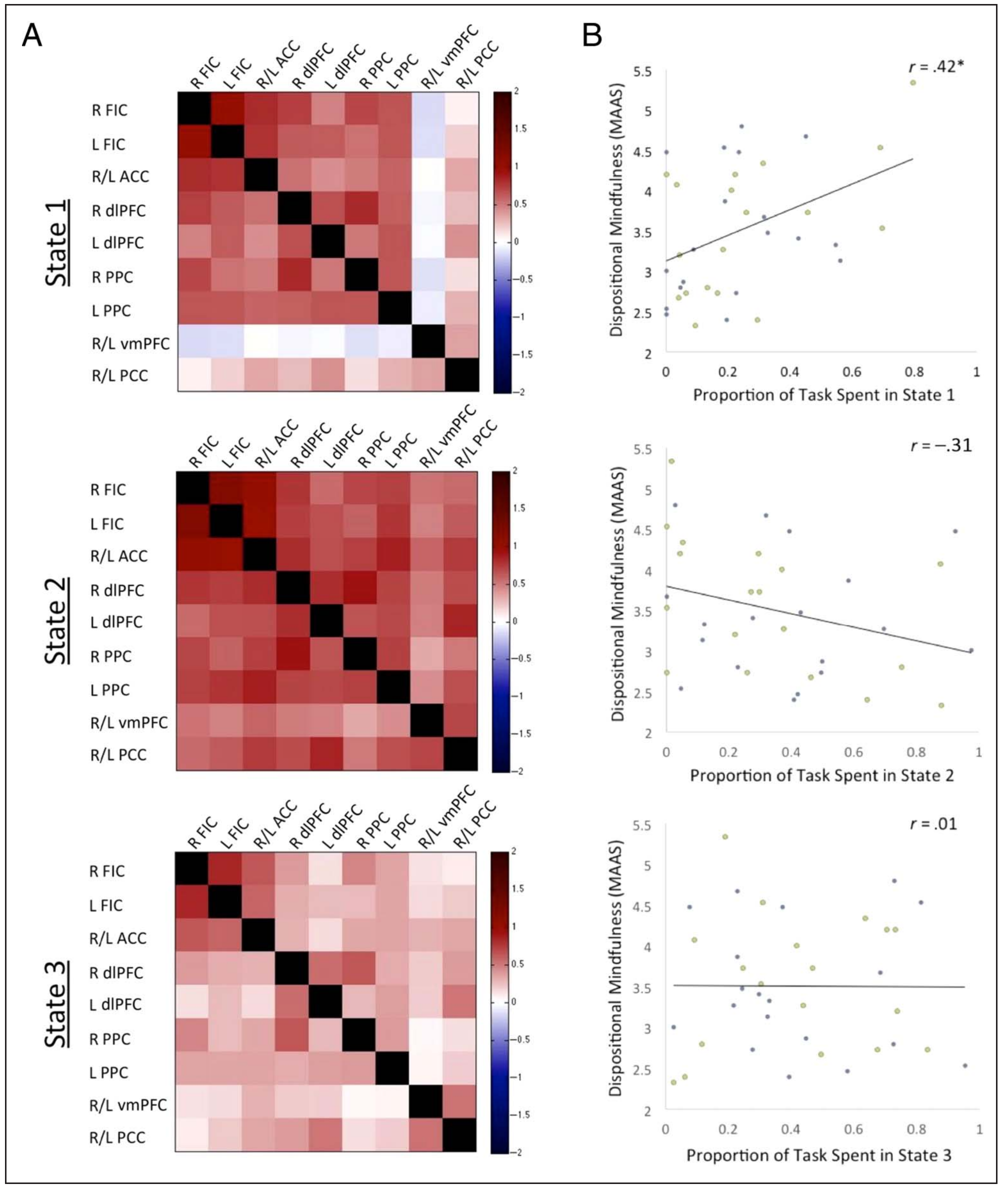

Figure 2. DFC state solutions via clustering. (A) The three state centrotypes produced via clustering with the nine bilateral ROIs. Color bar indicates Fisher r-to-z transformed FC values (red = positive correlation, blue = negative correlation). R = right hemisphere; L = left hemisphere. (B) Pretesting correlations between the proportions of time spent in each state and dispositional mindfulness scores for all participants. Blue data points represent intervention group participants; yellow points represent control group participants.

determine whether these states may be associable with mindfulness in a meaningful way, we assessed the correlation between the time spent in each state and participants' dispositional levels of mindfulness at pretesting.

Intervention Effects on Time Spent in Each State

We examined the effect of the intervention on the proportion of scan time spent in the DFC states associated with dispositional mindfulness by examining the Condition × Session interaction effect within a repeated-measures ANOVA (rmANOVA).

RESULTS

Functional States Defined by Clustering

k-Means clustering revealed three states of DFC during the mindful breathing task, each characterized by a distinct pattern of FC between the nine ROIs (Figure 2A). All three states demonstrate relatively strong positive correlations between regions within a given network, indicating that these networks showed strong within-network FC during the mindful breathing task.

State 1 demonstrates the hypothesized pattern of between-network FC for a state of focused attention: strong internetwork FC between regions of the EN and SN but decreased FC between these regions and regions of the DN, particularly the vmPFC. In support of the interpretation of this state's functional significance, participants exhibiting higher levels of dispositional mindfulness tended to spend a greater proportion of the mindful breathing task in this state at pretesting ($r = .42, p < .01$; Figure 2B).

State 2 expresses a pattern of between-network connectivity consistent with the corecruitment theory of mind-wandering: All nine regions show positive correlations with each other, indicating a coupling of EN, SN, and

DN activity. In support of this interpretation of the state's functional significance, participants exhibiting higher levels of disposition mindfulness exhibited a marginally significant tendency to spend less time in this state at pretesting ($r = -.31$, $p = .06$; Figure 2B).

Finally, State 3 shows strong within-network correlations (which are present in each of the states) but markedly reduced correlations between regions across the three networks. At pretesting, levels of dispositional mindfulness were not associated with the proportion of the task that was spent in this state. As such, the cognitive processes underlying this third state are less easily inferred; the FC values observed within this state could represent transitioning between states of focused attention and mind-wandering or perhaps reflect the average of a set of diverse but less frequent mental states that have been grouped together by the clustering procedure.

Focused Attention and Mind-wandering States of FC

Throughout the remaining portions of this article, we will refer to the first two states of the clustering solution as states reflecting focused attention and mind-wandering. These labels are supported by (1) previous work demonstrating the significant anticorrelation of default and executive regions during task focus (Hellyer et al., 2014; Wen et al., 2013; Gao & Lin, 2012; Brewer et al., 2011), (2) existing fMRI research demonstrating activation of both executive and default regions during mind-wandering (Fox et al., 2015; Christoff et al., 2009; Mason et al., 2007), (3) the correlations between state frequency and baseline dispositional mindfulness within this data set, and (4) the subsequently reported correlation between changes in the frequency of the focused attention state elicited by the intervention with changes in dispositional mindfulness. It should be noted, however, that these state descriptions are not definitive and are based on noncausal inference. In subsequent references to these states, we present the labels of focused attention and mind-wandering in quotation marks as a reminder of this inference.

State Differences in FC

To confirm the predicted and visually apparent differences in FC values between the "focused attention" (State 1) and "mind-wandering" (State 2) DFC states, we performed paired t tests to compare the FC values of the subject-level states at pretesting. FC values of internetwork ROI pairs that included a DN region exhibited prominent differences between the "focused attention" and "mind-wandering" states (Figure 3). The DN regions exhibited lower FC with regions from EN and SN within the "focused attention" state compared with the "mind-wandering" state. These differences were considerably larger than those observed for intranetwork FC values or internetwork FC between the EN and SN.

Intervention Effects on Dispositional Mindfulness and Brain States

The intervention placed considerable emphasis on cultivating the ability to focus attention through mindfulness

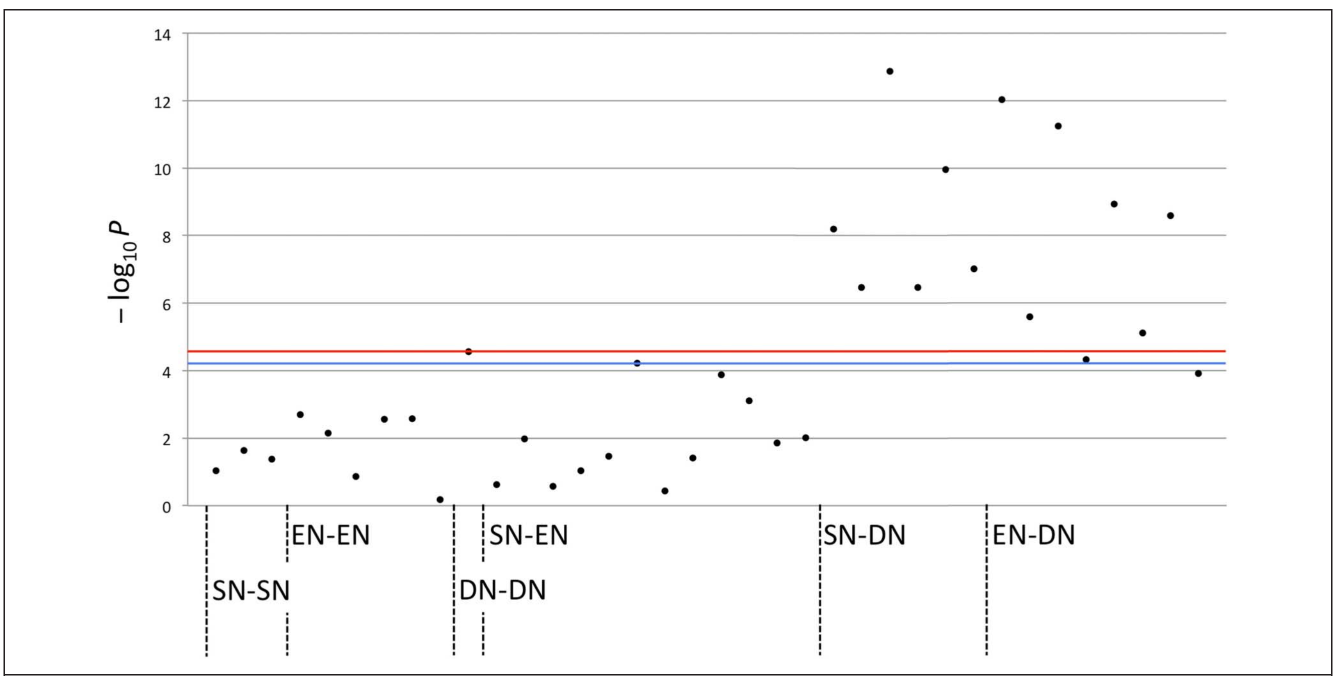

Figure 3. Manhattan plot of focused attention and mind-wandering state FC differences. Paired t tests were performed comparing each individual ROI pair's FC value within the focused attention and mind-wandering states. The y axis shows the $-\log_{10} p$ values of all 36 ROI pairs, and the x axis groups these pairs by their network affiliations. The horizontal red line represents the p value threshold for Bonferroni-corrected significance ($\alpha = .001$). The horizontal blue line represents the p value threshold corresponding to the false discovery rate ($q = 0.001$).

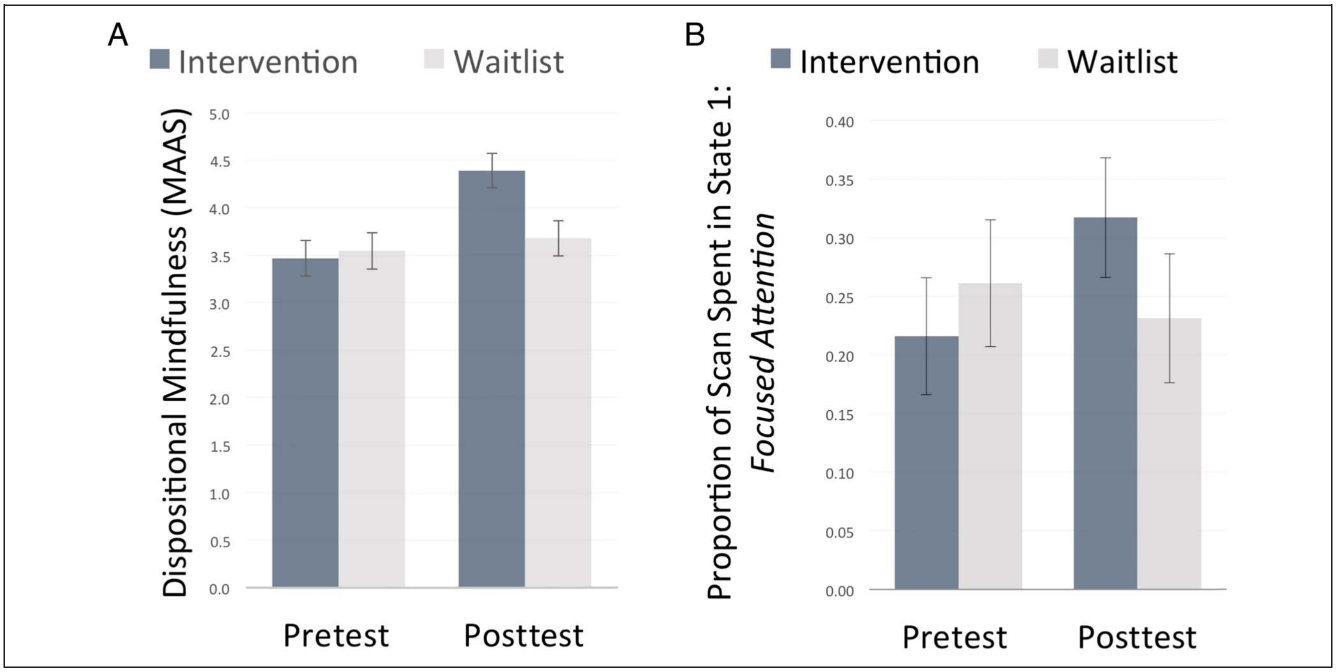

Figure 4. Intervention effects on mindfulness and the focused attention state. (A) Intervention-produced improvements in dispositional mindfulness were observed in the intervention group but not in the waitlist control group. (B) The intervention group, but not the control group, showed an increase in the proportion of the mindful breathing scan spent in the focused attention state (State 1) at posttesting. Error bars represent standard error.

training. We predicted that the intervention would lead to increases in dispositional mindfulness as reported by the MAAS. Before training, no significant differences in dispositional mindfulness were observed between conditions (p = .773). Using rmANOVA, we observed a significant Condition × Session interaction: Relative to the waitlist control condition, which did not change over 6 weeks, the intervention elicited substantial increases in dispositional mindfulness ($F(1, 35) = 16.363$, $p < .001$; Figure 4A).

Given these changes in dispositional mindfulness, we predicted that participants would spend an increased amount of time within the "focused attention" state during the postintervention mindful-breathing fMRI task. Indeed, rmANOVA revealed a Condition × Session interaction indicating that the intervention led to a significant increase in the proportion of time that the intervention group participants spent in the "focused attention" state, $F(1, 35) = 4.05$, $p = .05$ (Figure 4B). We also predicted that participants would spend less time in the "mind-wandering" state during posttesting; although intervention participants did spend a smaller proportion of time in this state during posttesting ($M = 0.28$) than pretesting ($M = 0.37$), the Condition × Session interaction was not significant, $F(1, 35) = 1.06$, $p = .31$. Although the third DFC state in the clustering solution did not demonstrate any relationship with the dispositional mindfulness measure at pretesting, we assessed whether it exhibited an intervention effect indicating a change in its frequency of occurrence. The third state did not show a significant interaction effect, $F(1, 35) = 0.22$, $p = .88$, indicating that its frequency of occurrence was not significantly affected by the intervention program.

We sought to determine if increases in the proportion of time spent in the "focused attention" state were associated with intervention-induced increases in mindfulness. Given the relatively small sample size for a within-condition analysis, we employed a rank order analysis that is more robust to deviations from normality and linearity than the Pearson correlation coefficient (Kasper, Cecotti, Touryan, Eckstein, & Giesbrecht, 2014; Kasper, Elliott, & Giesbrecht, 2012). This analysis iteratively compared pairs of participants within the intervention group to determine whether the person who improved more in dispositional mindfulness also increased more in the proportion of time spent in the state of "focused attention"; if so, the rank ordering was considered accurate. The rank order process was done for all possible pairs of participants to create an average accuracy, and a jackknife method that left out one participant for each cycle of comparisons was used to compute standard error. Rank order accuracies above chance (0.50) indicate a significant relationship between the changes across both variables. Tests of significance were computed using a one-sample t test against a null distribution of means equal to 0.50. Changes in dispositional mindfulness predicted changes in the proportion of time spent in the "focused attention" state from pretesting to posttesting within the intervention group, $t(18) = 4.78$, $M = 0.54$, $SEM = 0.02$, $p < .001$.

Although the "mind-wandering" state demonstrated a weaker relationship with the dispositional mindfulness measure at pretesting, we sought to determine whether the increases in dispositional mindfulness produced by the intervention were additionally associated with reductions in the proportion of time spent in the "mind-wandering" state. Rank order analysis indicated that, indeed, increases in dispositional mindfulness predicted reductions in the proportion of time spent in the "mind-wandering" state from pretesting to posttesting within the intervention group, $t(18) = 38.50$, $M = 0.65$, $SEM = 0.02$, $p < .001$.

DISCUSSION

We examined the DFC of brain regions within the DN, EN, and SN during a task of sustained attention to the sensations of breathing. This task was well suited to capture both moments of attentional focus and mind-wandering, and our intervention group was expected to improve on this task as a result of the formal mindfulness training within the intervention. It should be noted that, although we speculate that the formal mindfulness practice likely served as the predominant factor for producing the intervention-based effects presented here, the multifaceted nature of the intervention limits this assertion; other aspects of the intervention, such as stress reduction or exercise, may have contributed either independently or synergistically to the effects observed. On the basis of the dynamic patterns of FC during the mindful breathing task, we observed discrete FC states that may reflect "focused attention" (State 1) and "mind-wandering" (State 2). The state correlate of focus was characterized by positive FC between the executive and salience regions, which in turn showed reduced FC with default regions, particularly the vmPFC. By contrast, the state associated with mind-wandering exhibited positive FC between regions across all three networks.

The present findings are consistent with previous work demonstrating diverging time courses of activation across the default and executive control regions during cognitive tasks requiring focused attention (Hellyer et al., 2014; Wen et al., 2013; Gao & Lin, 2012; Brewer et al., 2011). The present findings also speak to an ongoing debate regarding the role of executive functions in mind-wandering. The corecruitment theory suggests that both the EN and the DN support mind-wandering and has been supported by neuroimaging studies that revealed the activation of both executive and default regions during mind-wandering (Fox et al., 2015; Christoff et al., 2009; Mason et al., 2007). The state associated with "mind-wandering" in our data displayed positive FC between DN and EN regions; although this relationship does not necessarily indicate that these regions were more active during mind-wandering (FC is not a measure of activation levels), our results provide supporting evidence that these networks may become synchronized in their activity during mind-wandering within an attentional task, suggesting cooperation between the networks.

The third state in our clustering solutions did not feature such strongly correlated salience and executive activity; in fact, this state was unique in its relative absence of strong internetwork FC overall. Because this state did not correspond meaningfully to levels of mindfulness at pretesting or show a pattern of FC readily interpretable in light of the existing literature, its interpretation is more ambiguous. Considering that the cognitive states of "focused attention" and "mind-wandering" may represent opposing ends of an attentional continuum, the third state could in principle reflect epochs of brain activity residing somewhere between these end points. The "focused attention" and "mind-wandering" states within our data set differ predominantly in their internetwork FC values involving the DN, so the observation that the third state features FC values largely in between those of the "focused attention" and "mind-wandering" states for these FC values lends support to this view. However, the third state features FC values among the EN and SN that are considerably lower and that do not fall between those observed in the DFC states of "focused attention" and "mind-wandering". Accordingly, it is also possible that this third state reflects a more diverse set of mental states that differ not only with regard to their position along a single attentional dimension.

Among those in the intervention condition, training led to increases in dispositional mindfulness across time that were associated with increases in the proportion of time spent in a state reflecting "focused attention" and decreases in the proportion of time spent in the "mind-wandering" state. Overall, these findings strengthen our supposition of the cognitive significance of these states and further demonstrate the ability of intervention programs to produce improvements in attention that are observable through DFC.

Limitations and Future Directions

The interpretation of these results rests on an inference about the functional significance of the observed DFC states. This inference is based on (1) convergence with existing fMRI research indicating that task focus is characterized by opposing patterns of activity across the DN and EN (Hellyer et al., 2014; Wen et al., 2013; Gao & Lin, 2012; Brewer et al., 2011), (2) consistency with fMRI research showing the activation of both DN and EN during mind-wandering (Christoff et al., 2009), (3) the correlation between the frequency of DFC states and dispositional levels of mindfulness, (4) the increase in frequency of the "focused attention" DFC state after training, and (5) the significant correlations between improvements in dispositional mindfulness and changes in the frequency of both the "focused attention" and "mind-wandering" DFC states. Although we believe that our interpretation is the most parsimonious account of these findings, it is limited by its correlational nature. These DFC states may reflect aspects of neural dynamics within key functional networks that support or enable these cognitive states rather than directly reflect the cognitive states themselves. Converging evidence could be provided by neuroimaging research that examines patterns of FC during focused attention and mind-wandering as revealed by experience sampling methods. The emerging capacity for real-time fMRI could provide even stronger support for our interpretation by soliciting self-reports of cognitive states when these DFC states occur, thus validating the correspondence between the first-person experience of focused attention or mind-wandering and these FC indices.

We intentionally limited the scope of our analyses to a priori ROIs from brain networks that are clearly relevant to the cognitive states we sought to characterize, but future research could include additional brain regions to more thoroughly characterize these mental states. The brain exhibits a modular and hierarchical organization in which large-scale networks are composed of multiple smaller-scale functional modules (Bullmore & Sporns, 2009), and thus, finer state distinctions produced by examining a broader set of regions may reveal states that differ according to subnetwork FC. In principle, a broad set of regions might even reveal distinct states of mind-wandering involving different thought content or emotional valence. However, the interpretation of each brain state's cognitive relevance may also become more difficult as the mosaics of FC values within individual states increase in complexity.

It is important to note that the state characterizations produced by DFC approaches are likely specific to the task being performed and the ROIs examined. Different cognitive tasks will place distinct demands on the networks examined, and therefore, the patterns of FC within states derived from other tasks will likely differ from the present states. Given the possible fractionation of intrinsic brain networks into modules and subnetworks, it is also likely that assessments of alternative regions from the same networks may produce somewhat different state results. Yet, although these sources of variability should be considered in future DFC applications, the present analyses demonstrate the potential of DFC approaches to elucidate the significance of fluctuating FC relationships within a task and to assess changes in brain dynamics across sessions.

Conclusions

Our attention shifts between focus and distraction countless times each day. These fluctuations profoundly influence what we experience, yet they are difficult to empirically observe and therefore to characterize. Emerging neuroimaging methods now allow for the characterization of discrete brain states based on patterns of FC even when external indications of these states are difficult or impossible to achieve. The present findings suggest that these methods can inform our understanding of (1) the neural correlates of cognitive states associated with focused attention and mind-wandering, (2) when these mental states occur, and (3) the ways these states are influenced by interventions. Considered in a broader context, these results point to the increasingly realistic possibility of decoding complex patterns of neural activity into a detailed account of the shifting mental states that make up the kaleidoscopic stream of our inner lives.

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Note

1. The observation of anticorrelated default and "task-positive" networks was made first by Fox et al. (2005). Other studies using data-driven methods have not consistently shown this anticorrelated activity (Mantini, Perrucci, Del Gratta, Romani, & Corbetta, 2007; Damoiseaux et al., 2006) given that this anticorrelation appears most robustly when shared variance between networks is removed via normalization. However, recent computational analyses based on anatomical connectivity and modeling of spontaneous network activity indeed predict such anticorrelated activity (Deco, Jirsa, McIntosh, Sporns, & Kötter, 2009; Ghosh, Rho, McIntosh, Kötter, & Jirsa, 2008).

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