Mind wandering and attention during focused meditation:
A fine-grained temporal analysis of fluctuating cognitive states

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Abstract

Studies have suggested that the default mode network is active during mind wandering, which is often experienced intermittently during sustained attention tasks. Conversely, an anticorrelated task-positive network is thought to subserve various forms of attentional processing. Understanding how these two systems work together is central for understanding many forms of optimal and sub-optimal task performance. Here we present a basic model of naturalistic cognitive fluctuations between mind wandering and attentional states derived from the practice of focused attention meditation. This model proposes four intervals in a cognitive cycle: mind wandering, awareness of mind wandering, shifting of attention, and sustained attention. People who train in this style of meditation cultivate their abilities to monitor cognitive processes related to attention and distraction, making them well suited to report on these mental events. Fourteen meditation practitioners performed breath-focused meditation while undergoing fMRI scanning. When participants realized their mind had wandered, they pressed a button and returned their focus to the breath. The four intervals above were then constructed around these button presses. We hypothesized that periods of mind wandering would be associated with default mode activity, whereas cognitive processes engaged during awareness of mind wandering, shifting of attention and sustained attention would engage attentional subnetworks. Analyses revealed activity in brain regions associated with the default mode during mind wandering, and in salience network regions during awareness of mind wandering. Elements of the executive network were active during shifting and sustained attention. Furthermore, activations during these cognitive phases were modulated by lifetime meditation experience. These findings support and extend theories about cognitive correlates of distributed brain networks.

Keywords: mind wandering, attention, meditation, default mode, subjectivity, fMRI

1. Introduction

A decade ago, seminal research demonstrated that a distributed neural network is active during the rest periods of neuroimaging experiments, when attention is not focused on the external environment (Gusnard et al., 2001; Raichle et al., 2001). This network, known as the task-negative or default mode network (DMN), consists of dorsal and ventral medial prefrontal cortex (PFC), posterior cingulate cortex and precuneus, posterior inferior parietal regions, lateral temporal cortex, and the hippocampal formation including parahippocampus (Buckner et al., 2008). Growing evidence suggests that the DMN is involved in internal mentation or stimulus-independent thought (Buckner et al., 2008; Gusnard et al., 2001; Raichle et al., 2001). Several reports have implicated the DMN specifically in mind wandering, a mental state that has been studied during undirected cognition, or intermittently during periods of sustained attention. In addition to mind wandering being informally reported as the bulk of conscious experience during rest (see Buckner et al., 2008), studies have found that people with a greater tendency to mind wander have higher activity in DMN regions during repetitive tasks (Mason et al., 2007), and that mind wandering identified through experience sampling during a sustained attention task is associated with DMN activity (Christoff et al., 2009). Based on the potential relationship of mind wandering states to such "default" neural activity, as well as informal reports of a high prevalence of mind wandering in daily life, it appears that this mental state constitutes a fundamental human conscious experience (Smallwood and Schooler, 2006). Despite the pervasiveness of mind wandering in the cognitive landscape, relatively little is known about its underlying neural mechanics.

In contrast to the DMN, a task-positive network is preferentially active when individuals are engaged in attention-demanding tasks focused on the external environment. This distributed network is made up of lateral PFC, premotor cortex, lateral parietal regions, occipital regions, anterior cingulate cortex (ACC), and insula (Fox et al., 2005; Fransson, 2005). A large body of task-based research implicates these brain regions as central to various aspects of attention (Corbetta et al., 2008; Fransson, 2005; Posner and Petersen, 1990). Functional connectivity studies have further shown that the DMN and attention networks fluctuate in an anticorrelated and regular pattern, which has led to the suggestion that these two brain networks may perform at least partially opposing functions (e.g., to alternately monitor the internal and external environment; Fox et al., 2005; Fransson, 2005). Scientific interest in these neural networks and their relevance to brain function is rapidly increasing; however, it remains unclear how ongoing activity in each network relates to subjective experience in real time.

Mind wandering often occurs at rest, but also frequently interrupts tasks requiring sustained attention, suggesting an interplay between cognitive states that may involve fluctuations between DMN and attention network activity (Smallwood and Schooler, 2006). The study of attention has a long history in cognitive science, and numerous accounts have been proposed. Much work, for example, proposes basic distinctions between component processes of attention, such as orienting, detecting targets, and maintaining altertness (Posner and Petersen, 1990; Posner and Rothbart, 2009). Other work establishes important attentional networks, including the dorsal and ventral attention systems (Corbetta et al., 2008; Corbetta and Shulman, 2002), the salience network, and the executive network (Seeley et al., 2007). Interestingly, there is also a long and detailed history of investigating attentional mechanisms through meditation in the Buddhist tradition (e.g., Gunaratana, 2002; Wallace, 2006), and an interdisciplinary scientific discussion has recently developed surrounding the possible cognitive and physiological mechanisms of meditation in light of its potential benefit for mental and physical health (Bishop, 2004; Chiesa, 2011; Chiesa and Serretti, 2010;

Hofmann et al., 2010; Ospina et al., 2007; Rubia, 2009). Some researchers have become interested in studying meditation as a means of understanding and possibly enhancing attention, beginning to synthesize ideas from these two fields (Jha et al., 2007; Lutz et al., 2009; MacLean et al., 2010; Zeidan et al., 2010).

Building on this previous work, we have developed a cognitive model of the natural dynamics between mind wandering and attention that occur during a common attention-based meditation practice. The practice of focused attention (FA) meditation is intended to help the practitioner enhance awareness of his/her cognitive states while developing attentional control (Lutz et al., 2008). Indeed, recent research has demonstrated that FA meditation improves attentional skill in several domains (Jha et al., 2007; Lutz et al., 2009; MacLean et al., 2010; Zeidan et al., 2010). During FA practice, an individual attempts to maintain focus on a single object (e.g., the breath), bringing attention back to the object whenever the mind wanders (Gunaratana, 2002; Wallace, 2006). In line with many traditional accounts, our model proposes that during FA meditation, one's subjective experience follows the structure outlined in Fig. 1a. When attempting to sustain focus on an object, such as the breath, an individual inevitably experiences mind wandering. At some time during mind wandering, the practitioner becomes aware that his/her mind is not on the object, at which point he/she disengages from the current train of thought and shifts attention back to the object, where it stays focused again for some period of time. As Fig. 1a illustrates, we have termed these states MW (representing mind wandering, or loss of focus), AWARE (representing the awareness of mind wandering), SHIFT (representing shifting of focus back to the breath) and FOCUS (representing maintenance of attentional focus on the breath).[1] The subjective experience of these states is a cyclical process that iterates repeatedly throughout a session of FA meditation.

Thus, the practice of FA meditation is not a single cognitive state, except perhaps in very advanced practitioners. Instead, it is a dynamic fluctuation between states of FOCUS and MW, incorporating the more transitory states of AWARE and SHIFT. In this regard, FA meditation involves a type of multitasking, or voluntary task switching between MW and FOCUS (Meyer, 2009). Traditional voluntary task switching paradigms allow participants to select the task they will perform on any given trial (Arrington and Logan, 2004), and recent work has implicated numerous attentional brain regions in task choice and cognitive shifting based on subjective volition (Forstmann et al., 2006; Forstmann et al., 2007). However, the present paradigm differs in that there is one explicitly stated task or goal (i.e., to keep the attention on the breath) and the alternate mental state arises naturally as a distraction rather than a chosen "task," per se.

With continued practice of FA meditation, individuals increase their capacity to become consciously aware of internal mental states (Lutz et al., 2008), suggesting that experienced meditators may be particularly well suited to report accurately on them. In this way, FA meditation provides an excellent paradigm for gathering subjective data to inform the study of phenomenological states such as mind wandering and attention, together with the shifts between them.

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[1] While we have attempted to develop a model that is broadly applicable across subjects, significant individual variability undoubtedly exists in the precise temporal nature of the cognitive fluctuations examined here. It is not our intention to suggest that each of these states has a consistent duration, or will always occur in a strict serial manner; instead our idealization is necessary for analytical purposes (see Materials and Methods). As these mental states will actually occur over variable lengths of time, some level of smearing between phases is inevitable within this model (Meyer et al., 1988). Further, the arrows between these states (Fig. 1a) represent transitional mental processes that enable the subsequent states, but are not expressly distinguished in the model, although they could be potentially. For more on these issues, see sections 4.1.5 and 4.5.

A better understanding of the dynamics between mind wandering and attention would have importance for numerous clinical populations in which these processes and associated networks are dysregulated (reviewed in Broyd et al., 2009; Buckner et al., 2008), in addition to informing the fields of education, human performance, and basic cognition. From this perspective, the goal of the study reported here was to further our understanding of the relationship between mind wandering and various aspects of attention, with an emphasis on the underlying neural correlates. Of particular interest was developing greater understanding of how individuals become aware of mind wandering and shift their attention so that they can remain engaged in a task.

The present study investigated these cognitive states using a subject-determined approach to fMRI analysis. We asked experienced meditation practitioners to perform 20 minutes of breath-focused FA meditation while undergoing fMRI scanning, with instructions to press a button whenever they realized their mind had wandered, and then return their focus to the breath. Thus, the button presses in this task provided temporal information on moments when practitioners experienced naturally occurring awareness of mind wandering. As Fig. 1b illustrates, we used these button press events to model four brief intervals in our fMRI analysis, following the theoretical model in Fig. 1a: MW, AWARE, SHIFT, and FOCUS. Across participants and events, this analytical model allowed us to establish the brain activations associated with these four intervals. We predicted that this cognitive cycle described in the model would reflect an alternation of activity between the DMN and task-positive attention network, as indicated by the dashed line and grey text in Fig. 1a. Specifically, we predicted that the DMN would be active during mind wandering periods, and that awareness, re-orienting, and maintenance elements of the task-positive attention network would be active during AWARE, SHIFT and FOCUS periods. As described earlier in Footnote 1, this model is not intended to be a complete or fully accurate account of these mental processes; rather, it is offered as a first step towards a greater understanding of fluctuating cognitive states, and its limitations are discussed throughout this report.

2. Materials and Methods

2.1 Participants

Fourteen healthy right-handed non-smoking meditation practitioners, ages 28-66 (3 male), were recruited from local Atlanta meditation communities (see Supplemental Materials for information on specific contemplative traditions). All participants signed a consent form approved by the Institutional Review Board at Emory University and the Atlanta Veterans Affairs Research and Development Committee as an indication of informed consent. Participants were assessed for meditation experience to estimate lifetime practice hours and ensure familiarity with breath-focus meditation. The FA meditation studied here is a basic, foundational practice in each of the contemplative traditions in which these participants were trained (Lutz et al., 2008). Exclusion criteria were: less than one year of regular meditation practice, fMRI contraindications, current substance dependence, history of sustained loss of consciousness, major neurological or medical illness, left-handedness, pregnancy, or history of major mental illness (as assessed by the Structured Clinical Interview for DSM-IV, Axis-I, Non-Patient version; First, 2001).

2.2 Meditation Task

Participants were asked to meditate for 20 min in the scanner by maintaining focused attention on the breath (specifically on the sensations of the breath on the nostrils and upper lip), keeping the eyes closed. They were instructed to press a button whenever they realized their mind had wandered away from the breath, and then return their focus to the breath. Mind wandering was construed as noticing when the mind was *completely* off the breath, being fully absorbed in a train of thought. Emphasis was not placed on speed or accuracy of reporting, other than to press the button "as soon as they realized" the mind had wandered; based on informal reports from the participants, we estimate that the time between awareness and button press was generally less than one second. Participants were trained outside the scanner on this task (in the presence of an audio file of scanner noise for acclimation), and practiced it during their regular meditation several weeks prior to the scan. To estimate brain activity associated solely with the button press, a motor control task was also performed following the meditation task (see Supplemental Materials). To assess whether respiration was associated with meditation experience, respiration data were collected during the initial practice session in the lab (Biopac Systems, Golecta, CA) and during the scan (In Vivo Research, Orlando, FL). Participants were all familiar with basic breath-focus meditation, readily understanding and performing the task.

Based on the idealized model of cognitive fluctuations presented in Fig. 1a, we constructed a cognitively defined baseline and three 3-second intervals surrounding each button press (see Fig. 1b). The duration of these intervals was based on participants' self-report of perceived time to become aware of mind wandering and return the focus to the breath, constrained for analyses purposes by the 1.5 sec scan TR (i.e., the time to acquire a set of 2D slices covering the brain). While the 3-second duration of intervals was therefore somewhat arbitrary, results obtained using this model were robust, suggesting they provided reasonable approximations of the relevant network activity underlying the model's four idealized phases. The TR containing the button press, as well as the preceding TR, made up the

AWARE phase, corresponding to awareness of mind wandering (3 sec total). The two TRs (3 sec) before the AWARE phase were cognitively defined as MW, representing mind wandering or loss of focus, and were treated as baseline in the general linear model (GLM).[2] The two TRs (3 sec) after the AWARE phase made up the SHIFT phase, representing the shifting of attention back to the breath. Finally, the two TRs (3 sec) following the SHIFT phase made up the FOCUS phase, representing maintenance of FA on the breath. A 6-second regressor of no interest after the FOCUS phase was included to model hemodynamic response function (HRF) time courses. Importantly, all time points not included in one of these phases were censored from the analysis, as they contained data that corresponded to undefined mental states. This censoring strategy was used to reduce noise in the analysis as much as possible. When two button press events occurred within 18 seconds, thereby causing the modeled intervals to overlap, the first event was censored (14% of events) and the second was used for analysis.

2.3 Functional MRI Analysis

Images were collected at the Emory Biomedical Imaging Technology Center on a 3T Siemens Trio scanner using a 12-channel head coil and preprocessed using standard methods in AFNI (Cox, 1996; see Supplemental Materials for scan parameters and pre-processing details). For each subject, a beta value was obtained at each voxel for conditions of interest by fitting a GLM to each subject's percent signal change data. The GLM included: 1) regressors for three conditions of interest (AWARE, SHIFT and FOCUS) modeled by convolving box car functions of the relevant time frame with a canonical gamma HRF (the fourth phase, MW, was

[2] From an analytical perspective, any one of the phases could be used as baseline, and use of another phase would also yield valid results. MW was chosen as baseline in this model because we viewed it as the most cognitively distinct from the other three phases, which all involve attentional processes.

the baseline); 2) a basis set of 2nd order polynomial functions, modeling low-frequency confounds; and 3) the subject's motion parameters, treated as confounds. A separate GLM was used to analyze the motor control task (Supplemental Materials). To investigate the possibility of confounds from respiration, the same regression analysis described above was performed including additional regressors that modeled respiration for the 11 subjects with available physiological data (Birn et al., 2006; Supplemental Materials); results of these analyses suggest that respiration did not significantly impact the findings obtained (Supplemental Fig. 1).

The betas for the conditions of interest from each participant's regression analysis were warped to Talairach space in preparation for group analyses. The warped betas for each of the 14 participants were then entered into a second-level random effects ANOVA with conditions of interest as fixed effects and subjects as a random effect. Relevant contrasts were also calculated at this stage for the motor control task in a separate ANOVA (motor-visual; see Supplementary Materials). The voxel-wise significance level was $p < 0.005$ with a spatial extent threshold of 612 mm^3 (17 functional voxels), yielding a whole-brain threshold of $p < 0.05$ corrected for multiple comparisons using AFNI AlphaSim. Only the AWARE phase was thresholded differently; a voxel-wise threshold of $p < 5.0 \times 10^{-6}$ was necessary due to highly robust activations.

2.4 Correlations with Meditation Experience

To investigate whether practice time (estimated lifetime hours of meditation experience) was associated with brain activity during the meditation task, we entered the number of hours for each subject as a covariate in an ANCOVA for each phase (AWARE, SHIFT and FOCUS, after removing MW baseline). As described in the Results, a region of interest in the ventromedial PFC emerged from this analysis; this area was found to be less active during the SHIFT phase as participants' meditation experience increased. Because of this area's relevance in mind wandering, and also in evaluative and self-related thought (see below), HRFs for each subject in this region were modeled. Specifically, a new GLM was fitted to each subject's percent signal change data, where the HRF from the beginning of the SHIFT phase was now modeled with a basis set of nine cubic splines spaced one TR (1.5 s) apart. The set of fitted splines was then temporally resampled in seconds, and averaged within the ventromedial PFC cluster for subjects with high and low practice times. Participants were dichotomized into high and low practice groups, as practice time was distributed bimodally in this sample, with 5 participants having >2000 hours of experience ("high practice") and 9 participants having <1200 hours ("low practice;" see Section 3.1). The HRF within the ventromedial PFC was compared between groups using a repeated-measures ANOVA, with time point in the HRF as the repeated factor and group (high vs. low practice) as the between-subjects factor. Alpha was set at 0.05.

3. Results

3.1 Behavioral Data

The average hours of estimated lifetime meditation practice across the whole group was 1386 hours (s.d. 1368). When participants were dichotomized into high and low practice groups, the average practice time for the high practice group was 3066 hours (s.d. 526); average practice time in the low practice group was 453 hours (s.d. 391), significantly less than the high practice group (t = 10.64, df = 12, p < 0.001). In the whole group, the average number of button presses during the meditation task was 15.5 (s.d. 7.4), representing an average of one reported mind wandering event every 80 seconds over the 20-minute meditation session. The number of button presses did not correlate significantly with practice time (r = -0.14, p = 0.64), and did not differ significantly between high and low practice groups (t = -0.40, df = 12, p = 0.70). The relatively low number of participants in this study combined with the need to censor some events when they overlapped (see Methods) may have limited our ability to find effects of practice time on the number of mind wandering events detected. It is also currently unclear how the ability to detect mind wandering, and the amount of mind wandering itself, changes with practice. For example, with expertise, fewer mind wandering events may occur, but the sensitivity to detect them may increase.

3.2 Physiological Data

Previous work has found that meditation experience can be correlated with respiration rate (Lazar et al., 2005). In the current sample, however, hours of practice did not correlate with respiration rate (breaths/minute) in the practice session (r = -0.16, p = 0.58), nor in the fMRI scan (r = -0.18, p = 0.60). Furthermore, respiration rate during meditation was not different between the high and low practice groups in the practice session (t = -0.70, df = 12, p = 0.50), nor the fMRI session (t = -0.46, df = 9, p = 0.66). Respiration also did not appear to influence fMRI signal in our paradigm (see Supplemental Materials for further details).

3.3 Imaging Data

As described earlier, we established four phases covering a 12-second window of time to represent the mental states of MW, AWARE, SHIFT, and FOCUS (3 seconds each, see Fig. 1 and Materials and Methods for details). Table 1 and Figure 2 report significant clusters for each phase contrasted against MW as baseline, along with clusters unique to MW (MW>SHIFT; no significant clusters were obtained from MW>AWARE or MW>FOCUS). During the AWARE phase, which contained the button press, we found expected motor-related activations in left sensory and motor regions when AWARE activations were overlaid with those seen during the motor functional localizer (red voxels in Fig. 2a). It should be noted that because the localizer task was performed outside the FA task context, cognitive and neural differences may exist between activity in the localizer and FA tasks. In addition to these activations, the largest activations in the AWARE phase were seen throughout bilateral anterior insula and dorsal ACC, with additional activations in bilateral midbrain, left superior parietal lobe and left superior/middle frontal gyrus. No significant deactivations were seen during the AWARE phase. In the SHIFT phase, right dorsolateral PFC and lateral inferior parietal regions were activated, with a smaller cluster in the left inferior parietal lobe. Additionally, bilateral clusters extending throughout areas of the thalamus and caudate were identified. Activation within the right dorsolateral PFC persisted during the FOCUS phase; no deactivations were found for this contrast. When compared to the SHIFT phase, the MW phase was associated with activations in default mode regions including posterior cingulate cortex, medial PFC, posterior parietal/temporal and parahippocampal regions. Additional bilateral activations during MW included pre- and post-central gyri, posterior insula and mid-cingulate/supplementary motor area.

Studies suggest that some meditation-related benefits are associated with the amount of practice a person has undertaken (Baron Short et al., 2010; Brefczynski-Lewis et al., 2007; Manna et al., 2010; Pace et al., 2009). To investigate the effect of meditation experience on brain activity in the four phases, we performed correlations between estimated lifetime hours of practice and activations in the AWARE, SHIFT and FOCUS phases (Table 2). The MW phase could not be assessed separately in the correlation analysis, given that it served as the baseline for the other three phases. During the AWARE phase, a cluster in the left inferior temporal gyrus was positively associated with practice time, indicating that more meditation experience was associated with more activity in this area (Supplemental Fig. 2). Practice time was negatively associated with activations in several clusters during the SHIFT phase (Fig. 3), indicating that more meditation experience was associated with less activity in this phase. These areas included ACC/ventromedial PFC, posterior insula, pre- and post-central gyri, striatum, thalamus and cerebellar regions. During the FOCUS phase, practice time was positively associated with activation in one cerebellar cluster.

Due to its implication in self-related and evaluative processing often associated with mind wandering (Legrand, 2009; Northoff and Bermpohl, 2004), we further investigated the ventromedial PFC cluster that was negatively correlated with practice time in the SHIFT phase (circled in Fig. 3a). A scatter plot between practice time and mean fMRI signal in this cluster confirmed a clear separation between groups (Fig 3b). When the HRF was modeled within this cluster, activation differed significantly over time between high and low practice groups, as assessed by repeated-measures ANOVA ($F(1,12) = 9.36$, $p = 0.010$), with activation decreasing over time in participants with high practice, and persisting in those with low practice (Fig. 3c).

4. Discussion

4.1 Activations during Cognitive Phases

Consistent with our proposed model of FA meditation in Fig. 1a, we detected activity in brain regions associated with the task-positive attention network during AWARE, SHIFT and FOCUS phases. Specifically, activations in these phases were consistent with results from previous research showing that the respective brain areas are associated with awareness (salience), re-orienting (executive control), and maintenance (sustained attention). We also detected activity during MW in brain regions frequently associated with the DMN, mentalizing and self-related processing. Below, we review the specific brain regions active for each phase of our model, relate them to previous findings, and examine their implications for the relationship between mind wandering and attention.

4.1.1 AWARE

During the AWARE phase, participants detected that their mind had wandered away from the attentional object, namely, the breath. We propose that the specific detected event in this paradigm is the mental state of mind wandering, which can also be viewed as a mismatch between the overarching goal of the meditation task (i.e., to keep attention on the breath) and the current state (i.e., the attention is not on the breath). In this sense, the detection of mind wandering represents a form of conflict monitoring, with the mind wandering state as a salient attentional target.[3]

Analysis of the AWARE phase revealed robust activations in bilateral anterior insula and dorsal ACC (in addition to expected motor-related activations, Table 1 and Fig. 2a). These regions are consistent with a subdivision of the attention network that has recently been referred to as the salience network (Seeley et al., 2007). Anterior insula and dorsal ACC show highly correlated activity during resting states and have been implicated in a diverse range of cognitive processes, including conflict monitoring and error detection, interoceptive-autonomic arousal, the moment of perceptual recognition, self-regulation, emotional aspects of pain, empathy, musical chills, pleasurable touch, and present moment awareness (reviewed in

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[3] It should be noted that due to the present temporal resolution of 1.5 seconds/TR, it is not possible to determine with certainty whether the brain activations during this phase are related to the *cause* of this detection, or the *act* of detection itself. However, given the available evidence about the function of the brain regions identified during this phase (above), we proceed under the assumption that these activations are related to the act of detection, rather than the cause.

Craig, 2009; Seeley et al., 2007; Singer et al., 2009). Detection of relevant or salient events is important in all the aforementioned processes, which has led to the suggestion that these brain regions, acting together, comprise a general salience network (Seeley et al., 2007). While most paradigms have implicated this network in the detection of external salient events, the detected event in our paradigm—a state of mind wandering—was internally generated and purely cognitive in nature. Our finding, therefore, extends the scope of the salience network and supports recent suggestions that it may indeed function to detect general salience, regardless of environment or modality (Corbetta et al., 2008; Craig, 2009; Seeley et al., 2007). Further, the strong involvement of anterior insula in this phase is very much in line with the recent hypothesis that this region underlies present-moment conscious awareness (Craig, 2009), which would arguably be a central feature of experiencing salience.

4.1.2 SHIFT

When participants were redirecting their attention from mind wandering content back to the breath during the SHIFT phase, we observed significant activation in lateral PFC (dorsal and ventral) and lateral inferior parietal cortex, with larger clusters and more robust activation in the right hemisphere (Table1, Fig. 2b). These frontoparietal regions are consistent with another subdivision of the task-positive attention network known as the executive network (Corbetta et al., 2008; Corbetta and Shulman, 2002; Seeley et al., 2007; Sridharan et al., 2008). These regions show correlated fluctuations at rest (Seeley et al., 2007; Sridharan et al., 2008), and have been well characterized during tasks requiring visual attention (e.g., target detection; Corbetta et al., 2008). The executive network acts on relevant stimuli (which are thought to be identified by the salience network) by re-orienting or directing attention while maintaining a goal (Corbetta et al., 2008; Corbetta and Shulman, 2002; Seeley et al., 2007).

Parietal elements of this network have been implicated specifically in attentional disengagement (Posner and Petersen, 1990), a process often accompanying re-orienting and also likely occurring during this phase. Thus, what is known about the function of this network corresponds well with the hypothesized cognitive processing occurring in this phase: shifting or re-orienting attention from mind wandering back to the breath.

4.1.3 FOCUS

During maintenance of attention in the FOCUS phase, a cluster in the dorsolateral prefrontal region of the executive network remained active from the SHIFT phase (Table 1, Fig. 2c). This may represent persistent neural activity underlying working memory, or keeping the goal in mind, to maintain sustained attention on the focal object (Curtis and D'Esposito, 2003; D'Esposito, 2007; Miller and Cohen, 2001). The dorsolateral PFC has been specifically implicated in active rehearsal, which consists of "the repetitive selection of relevant representations or recurrent direction of attention to those items" (D'Esposito, 2007). Active rehearsal would be central to the sustained attention we hypothesize is occurring in the FOCUS phase, providing repetitive selection of, or attention to, the breath. The lack of activation in parietal elements of the executive network during this phase may be related to the role of the parietal cortex in disengagement of attention rather than in focusing attention (Posner and Petersen, 1990). As mentioned above, attentional disengagement presumably occurred during the SHIFT phase when it was necessary to disengage from ongoing mind wandering content.

4.1.4 Mind wandering

Finally, during the MW phase, we detected activity in posterior cingulate cortex, medial PFC, posterior parietal/temporal cortex and parahippocampal gyrus (Table 1, Fig. 2d). While this study did not employ a task vs. rest paradigm for identification of DMN activity, these regions have been repeatedly associated with the DMN in prior studies (Buckner et al., 2008). This pattern supports our hypothesis that the DMN is associated with mind wandering, and is consistent with recent work that links them (Buckner et al., 2008; Christoff et al., 2009; Mason et al., 2007). Furthermore, this result is novel in identifying neural correlates of mind wandering using subjective report, rather than using experimental inductions or experience sampling probes. Considering recent evidence that increased DMN activity is associated with negative mental health outcomes (Grimm et al., 2009; Sheline et al., 2009), it is tempting to speculate that one mechanism through which meditation may be efficacious is by repeated disengagement or reduction of DMN activity.

In addition to DMN-related activity, we also detected MW activations in bilateral post-central gyrus and posterior insula, extending into pre-central and supplementary motor regions (Table 1, Fig. 2d). Some of these activations may represent motor planning processes that became active prior to the button press. Indeed, many of these regions were also active during the AWARE phase when the button press occurred (Table 2), and these same regions were also activated during the motor control task. Another possibility is that mind wandering states themselves involve these sensory and motor regions as subjects simulate being immersed in imagined situations. Posterior insula in particular has been associated with mind wandering (Christoff et al., 2009), and was also found to be more active during standard rest than FA meditation (Manna et al., 2010). Future research will be required to distinguish these possibilities.

4.1.5 Summary of Neural Correlates of Cognitive Phases

Taken together, these results suggest a pattern of fluctuating neural network activity during FA meditation that can be summarized as follows. Mind wandering periods are associated with activity in brain regions implicated in the DMN. At the moment when awareness of mind wandering occurs, the salience network becomes strongly active, perhaps from detecting the targeted mismatch between goal and current state. Subsequently, the frontoparietal executive network becomes active as participants disengage from mind wandering and redirect attention back to the breath, with dorsolateral PFC activity persisting during maintenance of attention on the breath. This pattern of shifting activity is consistent with an alternation between default mode and task-positive networks, in which DMN activity is associated with mind wandering states, and attentional subnetworks are associated with awareness, shifting attention, and maintaining attention. The present findings also highlight further divisions within the larger attention network, specifically between the salience and executive networks.

When speculating about the underlying subjective states associated with these neural activations, it is important to consider that each phase in the model likely includes a set of transitional mental processes, followed by a somewhat longer and more stable mental state that these transitional processes enable. In the AWARE phase, for example, one could distinguish between a transitional process of *becoming aware* and a more stable state of *conscious awareness*. The present model does not distinguish between transitional processes and subsequent cognitive states; therefore, it cannot be determined whether transitional processes, states, or both are associated with the identified brain activations. Further, it remains unclear what exactly enables this awareness at any given moment, or why awareness occurs at certain moments and not others. Such finer delineation of subjective experience could be investigated with methods allowing for better temporal resolution, along with improved classification algorithms. Alternatively, finer delineation might also be accomplished by using participants with sufficient introspective skill to provide accurate subjective report about such rapid and subtle shifts.

The respective findings that distinguish the four cognitive phases in Fig. 1a shed light on the neural underpinnings of the continual oscillation of mind wandering and FA. For example, a study that employed experience sampling to investigate mind wandering during a sustained attention task reported not only DMN activations, but also elements of the salience and executive networks (Christoff et al., 2009). One interpretation of this discrepancy with our findings is that the longer time window (10 sec) used by Christoff and colleagues to define mind wandering included other cognitive functions (e.g., detection of salient events and/or sustained attention on the task) that are associated with task-positive attentional networks. It is also possible, however, that different activation patterns are associated with probe-caught vs. self-caught mind wandering. For example, if some episodes of mind wandering include attentional activation, these episodes may escape self-catching because the attentional resources needed for awareness are already engaged. In contrast, experience sampling probes may detect these episodes, unlike a self-catching paradigm. Additionally, the nature of the contrasts used in the present study may have inadvertently masked the detection of attentional regions active during mind wandering. These possibilities highlight important areas for future studies to address when examining the inherently complex process of mind wandering and its interaction with task performance.

The present findings may also inform research on network dynamics. A recent study implicated the salience network (frontoinsular cortex and dorsal ACC) as playing a central role in switching between the DMN and executive network (Sridharan et al., 2008). In our paradigm, anterior insula and dorsal ACC were robustly active during the AWARE phase, thereby situating salience network activation temporally between activation of DMN regions and executive network regions. Although temporal order alone does not demonstrate conclusively that the salience network plays a causal role in network switching, these findings are in general agreement with the hypothesis that frontoinsular cortex may function as a neural switch between these two networks. In contrast to experimenter-determined paradigms (Sridharan et al., 2008), the present study utilized a subject-determined "network-switching" or cognitive shifting paradigm. Indeed, the practice of FA meditation intentionally highlights the cognitive shifts between mind wandering and FA in the mind of the practitioner, making it an ideal paradigm for application of the present model. It is likely, however, that these neural and subjective fluctuations occur in a similar manner during other tasks requiring sustained attention and characterized by frequent distraction. Future studies are necessary to investigate this possibility.

4.2 Relevance to Meditation Research

The last decade has seen a steady increase in efforts to understand how meditation affects the brain and body, in light of accumulating evidence about potential health benefits of contemplative practices (Chiesa and Serretti, 2010; Hofmann et al., 2010; Ospina et al., 2007; Rubia, 2009). The present study used a fine-grained temporal analysis of object-based FA meditation to investigate the neural differences between mind wandering and attention. Due to the lack of a comparison group of non-meditators, we cannot conclude that our findings are unambiguously associated with meditation practice; however, these findings nevertheless bear on the extant body of meditation research. To date, fMRI studies examining various types of meditation have utilized block designs, with blocks generally ranging from 3-20 minutes. While the block-design approach provides a high signal-to-noise ratio and is useful for detecting robust activations across an extended temporal duration, the averaging process effectively "washes out" the cognitive fluctuations that occur from moment to moment. In line with our findings, previous studies of focused/concentrative meditation have reported frontoparietal executive network activity during meditation (Baerentsen et al., 2010; Baron Short et al., 2010; Brefczynski-Lewis et al., 2007; Lazar et al., 2000). Importantly, however, studies have also implicated regions from salience and default networks as being active (Baerentsen et al., 2010; Baron Short et al., 2010; Brefczynski-Lewis et al., 2007; Hölzel et al., 2007; Lazar et al., 2000; Manna et al., 2010). These findings could reflect differences in the specific meditation practice employed, but may also be due to averaging across fluctuating cognitive states that engage the various brain networks differentiated here.

While the present results were derived from participants trained in meditation, we expect that this model will also apply to non-meditators. Recent studies show that novices can successfully engage in visually-based meditation practices (Brefczynski-Lewis et al., 2007) or present moment-based practices (Farb et al., 2007). An exciting avenue for future research will be to explore the utility of this paradigm to investigate real-time cognitive fluctuations in healthy non-meditators, as well as in various clinical populations. For example, individuals with ruminative depression or attention deficit disorder may exhibit altered spatial or temporal patterns of neural activity during the phases of this paradigm, or different frequencies of detected mind wandering events. Comparison of these and other clinical populations to healthy controls and meditation practitioners may allow for insights into the neural underpinnings of mental diseases, and help us understand the relationship of meditation to mental health.

4.3 Practice Time Effects

Previous research indicates that meditation effects may be associated with the amount of contemplative practice a person has experienced (Baron Short et al., 2010; Brefczynski-Lewis et al., 2007; Manna et al., 2010; Pace et al., 2009). In our paradigm, activity in several brain regions was significantly correlated with practice time, especially during the SHIFT phase (Table 2).[4] The cognitive processes occurring during this phase—disengaging and re-orienting of attention—are some of the primary cognitive skills that FA meditation trains. All correlations in this phase were negative, signifying lower neural activity in participants with more meditation experience. These findings may reflect an overall practice effect whereby performance of well-learned tasks requires less neural activity, as has been suggested previously with regard to meditation experience (Brefczynski-Lewis et al., 2007). Indeed, as discussed below, more experienced meditators may have been faster at completing the re-orienting operations associated with the SHIFT phase.

We were especially interested in the ventromedial PFC cluster during the SHIFT phase, given the proposed involvement of this region in evaluative (Legrand, 2009) and self-related processing (Northoff and Bermpohl, 2004) associated with the DMN. Investigation of the BOLD response within this cluster over time revealed that, in the high practice group, activity in this region fell below baseline levels after the button press, whereas activity persisted in participants with low practice time (Fig. 3b). These findings may indicate that more meditation experience allows for a faster or more efficient disengagement of cognitive processes subserved by this region. While these interpretations are necessarily speculative, one possibility is that experienced meditators are better able to terminate ongoing mind

[4] Regions appearing in this correlational analysis may differ from those that show significant activations in the whole-group analysis (Table 1) due to the differing nature of the statistical models used. For example, as seen in Figure 3, if some participants show positive activations and others show deactivations, the group average will be near zero.

wandering content, as this medial PFC region is part of the DMN and has been strongly implicated in mind wandering (Buckner et al., 2008; Fox et al., 2005; Fransson, 2005). Further, meditators with more experience may have an increased ability to disengage from, or have a reduced likelihood of, self-evaluation or judgment (Legrand, 2009; Northoff and Bermpohl, 2004) that is often experienced immediately after the realization of mind wandering (e.g., "I'm not good at this, I can't keep my mind focused"). These kinds of judgmental thoughts are common when beginning to learn meditation, but most practices emphasize the importance of non-judgmental awareness, and encourage dissociation from these kinds of thoughts (e.g., Kabat-Zinn, 2003). Functional connectivity analyses may shed light on how repeated meditation could produce such changes (e.g., by increasing or decreasing relevant network connectivity); results of these analyses will be published in a separate paper. It should be noted that the measures used here are necessarily relative in nature, and it is possible that participants in the high practice group had greater activity in this region before mind wandering detection, rather than less activity after. This possibility, however, seems counterintuitive in that it would suggest more DMN activity/mind wandering in the high practice participants, which is contrary to many traditional and anecdotal accounts of meditation training (Gunaratana, 2002; Wallace, 2006). In general, longitudinal studies within subjects over the course of meditation training are needed to more fully understand the plasticity that occurs with repeated practice, and recent work in this area shows promise (Holzel et al., 2011; Tang et al., 2010).

4.4 Methodological Implications

From a methodological perspective, it is encouraging that we were able to detect robust activations using an idealized cognitive model, a fairly small number of participants, short temporal intervals, and a moderate number of events. It may be that our analytical approach, using a very narrow time window during which we could be relatively certain of mental states, resulted in a favorable signal-to-noise ratio. Thus, by relinquishing experimental control in favor of subjective input from a trained participant population, it may be possible to retain or even enhance the ability to detect neural correlates of distinct cognitive states. This is promising for moving subjective methods forward in neuroimaging research, and provides impetus for the extension and development of other neurophenomenological paradigms (Lutz and Thompson, 2003).

4.5 Potential Caveats and Limitations

There are several important limitations of the present work. The paradigm we employed is inherently limited by the lack of knowledge about when the transition from FOCUS to MW occurs. Only approximate temporal information as to the *awareness* of mind wandering can be obtained, a moment that occurs at some variable time after mind wandering begins. To control for this in the present study, we censored from the analysis all time points that did not fall into one of the defined phases (Figure 1b), and only examined a brief window of time during which we could be relatively certain that the relevant cognitive events were occurring. Even so, this certainty remains limited, and we cannot ensure that the presumed cognitive states occurred during the associated phases in every case. In reality, it is likely that these cognitive states occur over differing amounts of time across events within one subject, as well as between subjects, introducing variability that will lead to some level of smearing between phases (Meyer et al., 1988). In particular, the AWARE and SHIFT phases, each being bracketed by two other phases, are the most susceptible to this smearing effect. Further, from both a subjective and a modeling perspective, it is also possible that some of the states we propose may occur at least partially in parallel, rather than in a strict serial order (Fig. 1a). If so, then even further smearing is introduced into this kind of data. Additionally, it was not possible to evaluate non-neural influences on the fMRI signal that may be time-locked to self-caught mind wandering and that may be influencing our results (e.g., autonomic nervous system changes).

Given these possibilities, the present theoretical conclusions are open to alternative interpretation and should be viewed as tentative at this time. Nevertheless, the cognitive phases as presently defined correspond with brain activations that are well known to be involved in the mental processes hypothesized to be occurring. Thus, we hope that this approach represents a productive step towards developing more sophisticated models of complex cognitive phenomena associated with focused attention and accompanying mind wandering.

4.6 Conclusions

Because mind wandering and sustained attention represent fundamental cognitive activities, increasing our understanding of their relationship has importance for both basic and clinical science. Here we have identified fluctuations between distinct neural networks that are associated with the state of mind wandering, as well as with its detection and the ability to return to FA during an ongoing attentional task. Results of this study also shed light on the neural correlates of dynamic cognition during FA meditation, and suggest that repeated meditation practice may alter relevant brain networks. Finally, this study provides a method in which first-person subjective information can be used in fMRI paradigms to reveal a finely detailed picture of cognitive states as they fluctuate in real time. Future studies should continue to explore the use of subjective report to gain a more detailed understanding of ongoing conscious experience, along with the nature of mind wandering and attention.

Acknowledgements

We extend our warm gratitude to John Dunne, Guiseppe Pagnoni and Waqas Majeed and Jaemin Shin for their input on the design and analysis for this study. We also thank David Meyer and two anonymous reviewers for thoughtful comments on an earlier draft of the manuscript. This work was supported by a Francisco J. Varela Award from the Mind and Life Institute, the Emory Neuroscience Initiative and the Atlanta Veterans Affairs Medical Center.

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Abbreviations

DMN: default mode, FA: focused attention, PFC: prefrontal cortex, ACC: anterior cingulate cortex, HRF: hemodynamic response function, GLM: general linear model.

(For tables) R: right, L: left, ACC: anterior cingulate cortex, dlPFC: dorsolateral prefrontal cortex, IFG: inferior frontal gyrus, MFG: middle frontal gyrus, PCC: posterior cingulate gyrus, SFG: superior frontal gyrus, SMA: supplementary motor area, vmPFC: ventromedial prefrontal cortex.

Figure Captions

Figure 1. Theoretical and analytical models of FA meditation. A) Theoretical model of dynamic cognitive states experienced during a session of FA meditation. A detailed description of this cognitive cycle is presented in the Introduction. The grey dashed line represents our hypothesized division between DMN and task-positive attention network activity during these states. B) Analytical model for construction of phases surrounding each button press (represented by the heavy black vertical line). While the button press is represented here in the middle of a TR, note that the timing of the button press within a TR will be variable. A detailed description of the phases is presented in Materials and Methods.

Figure 2. Significant activations for phases of interest. Specific contrasts are listed in each panel. A) Activations during the AWARE phase are in green (due to highly robust activations, this contrast was thresholded to $p < 5.0 \times 10^{-6}$). Voxels that were also significantly active during the motor control task (motor > visual; $p < 0.005$) are shown in red. Prominent activity was detected in dorsal ACC and frontoinsular cortex. B) Activations in lateral PFC and posterior parietal regions during the SHIFT phase. C) Activation in dorsolateral PFC during the FOCUS phase. D) Activations during MW phase included elements of DMN, as well as sensory and motor cortices and posterior insula.

Figure 3. Practice time effects. A) Several clusters that were negatively correlated with practice time during the SHIFT phase. The ventromedial PFC cluster that was examined in B ad C is circled. B) Scatter plot of the relationship between practice time and fMRI signal in the ventromedial PFC cluster. Participants with high and low practice time are clearly segregated.

C) Time courses from the ventromedial PFC cluster were extracted, and HRFs were calculated from the onset of the SHIFT phase for each subject. Percent signal change (from MW, mean ± s.e.m.) over time is plotted for high (N=5) and low (N=9) practice participants. The BOLD response is significantly reduced in high practice compared to low practice participants across the modeled time series. * Main effect of group over time by repeated-measures ANOVA, p = 0.010.

Table 1. Activations during Conditions

	Brodmann area	Volume (mm^3)	Peak			mean *t*-value
			X	Y	Z	
AWARE > MW[a]						
L Pre/Postcentral Gyrus, L Posterior Insula	1,2,3,4,13	6621	-43	-30	38	8.26
R Anterior/Middle Insula	13,47	5629	38	0	-1	8.29
Dorsal ACC	24,32	4177	-9	5	31	8.02
L Anterior/Middle Insula	13,47	3779	-32	20	-1	8.35
Midbrain	-	1221	-6	-19	-17	7.95
L Superior Parietal	7	1221	-29	-53	59	8.26
L SFG/MFG	10	846	-28	48	24	7.88
SHIFT > MW						
R dlPFC/SFG/MFG/IFG	8,9,10,46	7545	42	54	14	4.39
L Caudate Body/Thalamus	-	4598	-13	-9	26	4.25
R Caudate Body/Thalamus	-	4291	24	-13	8	3.72
R Inferior Parietal	40	3641	55	-41	44	3.90
L Inferior Parietal	40	733	-45	-56	57	3.63
R MFG	9	697	41	35	39	3.64
FOCUS > MW						
R dlPFC/MFG	9	923	42	32	34	4.22
MW > SHIFT						
R Posterior Insula, Pre/Postcentral Gyrus	1,2,3,4,13	15873	48	-30	22	4.13
L PCC, Cuneus, Precuneus, Lingual Gyrus	19,30,31	13422	-18	-58	16	4.29
L Posterior Insula, Pre/Postcentral Gyrus	1,2,3,4,13	11873	-50	-18	51	3.94
R PCC, Cuneus, Mid-occipital/Lingual Gyrus	30,35,18	7658	24	-93	13	3.83
Mid-cingulate Gyrus, Paracentral Lobule	6	7368	-14	-8	48	3.87
L Middle Temporal Gyrus	39	5099	-36	-81	19	3.89
R Middle Temporal Gyrus	39	3083	49	-76	17	3.85
Medial PFC/Ventral ACC	32,24	2656	1	32	-10	4.02
R Parahippocampal Gyrus	35,36	1291	26	-28	-13	4.27
L Superior Temporal Gyrus	22	1031	-50	-10	-4	3.79
L Parahippocampal Gryus/Uncus	36	746	-26	-8	-26	3.95

Activatons in clusters for cogntitive conditions (significant at $p<0.005$, 17 functional voxels, 612 mm^3). *t*-values are absolute values. a: This contrast was thresholded to $p<5.0$ x 10-6. R: right, L: left, ACC: anterior cingulate cortex, dlPFC: dorsolateral prefrontal cortex, IFG: inferior frontal gyrus, MFG: middle frontal gyrus, PCC: posterior cingulate gyrus, SFG: superior frontal gyrus.

Table 2. Correlations with Practice Time

	Brodmann area	Volume (mm^3)	Peak X	Peak Y	Peak Z	Mean *r*-value
AWARE						
L Inferior Temporal Gyrus	20	690	-44	-6	-35	0.76
SHIFT						
Paracentral Lobule, SMA, Pre/Postcentral Gyrus	4,6,24,31	10636	3	-10	46	-0.75
R vmPFC/ACC	10,32	1952	16	53	-1	-0.74
R Cerebellar Culmen and Declive	-	1695	10	-59	-14	-0.77
L Putamen, Thalamus, Subthamamic Nucleus	-	1341	-20	-1	-6	-0.75
R Cerebellar Culmen	-	1110	33	-42	-26	-0.75
R Middle Temporal Gyrus		993	42	-42	5	-0.72
L Posterior Insula	13	986	-47	-22	20	-0.77
R IFG, Anterior Insula	47,13	854	30	13	-12	-0.77
L Cerebellar Declive	-	798	-12	-56	-20	-0.74
L IFG	45,46	702	-59	21	19	-0.75
L SMA	6	653	-10	-11	64	-0.75
R Putamen	-	651	33	-2	8	-0.75
FOCUS						
R Cerebellum (Nodule and Uvula)	-	743	7	-57	-27	0.77

Clusters that were correlated with practice time (significant at $p<0.005$, 17 functional voxels, 612 mm^3). R: right, L: left, ACC: anterior cingulate cortex, dlPFC: dorsolateral prefrontal cortex, IFG: inferior frontal gyrus, PCC: posterior cingulate gyrus, SMA: supplementary motor area, vmPFC: ventromedial prefrontal cortex.

Figure 1

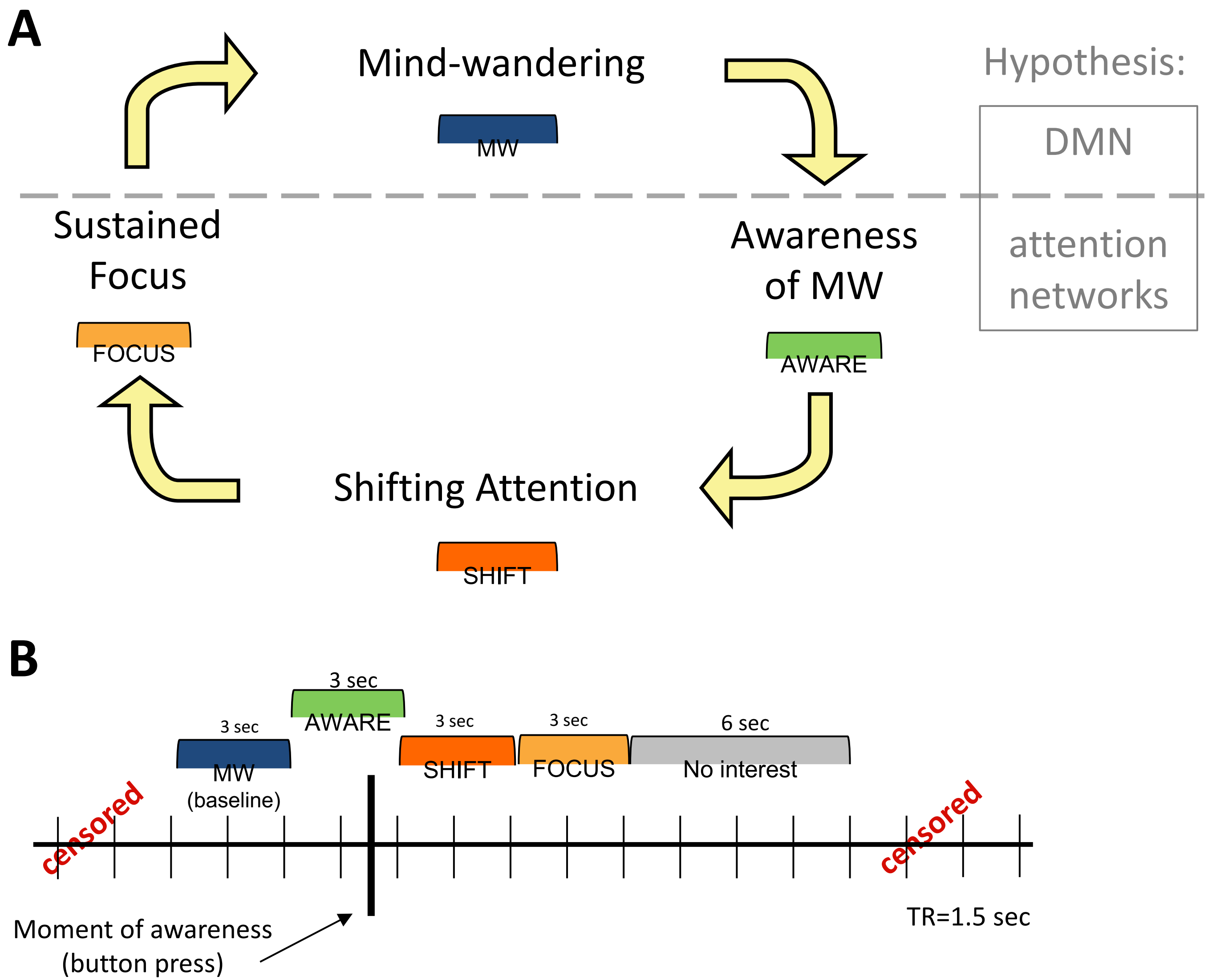

A
Mind-wandering
MW
Hypothesis:
DMN
attention
networks
Sustained
Focus
FOCUS
Awareness
of MW
AWARE
Shifting Attention
SHIFT
B
3 sec
AWARE
3 sec
MW
(baseline)
3 sec
SHIFT
3 sec
FOCUS
6 sec
No interest
censored
censored
Moment of awareness
(button press)
TR=1.5 sec

Figure 2

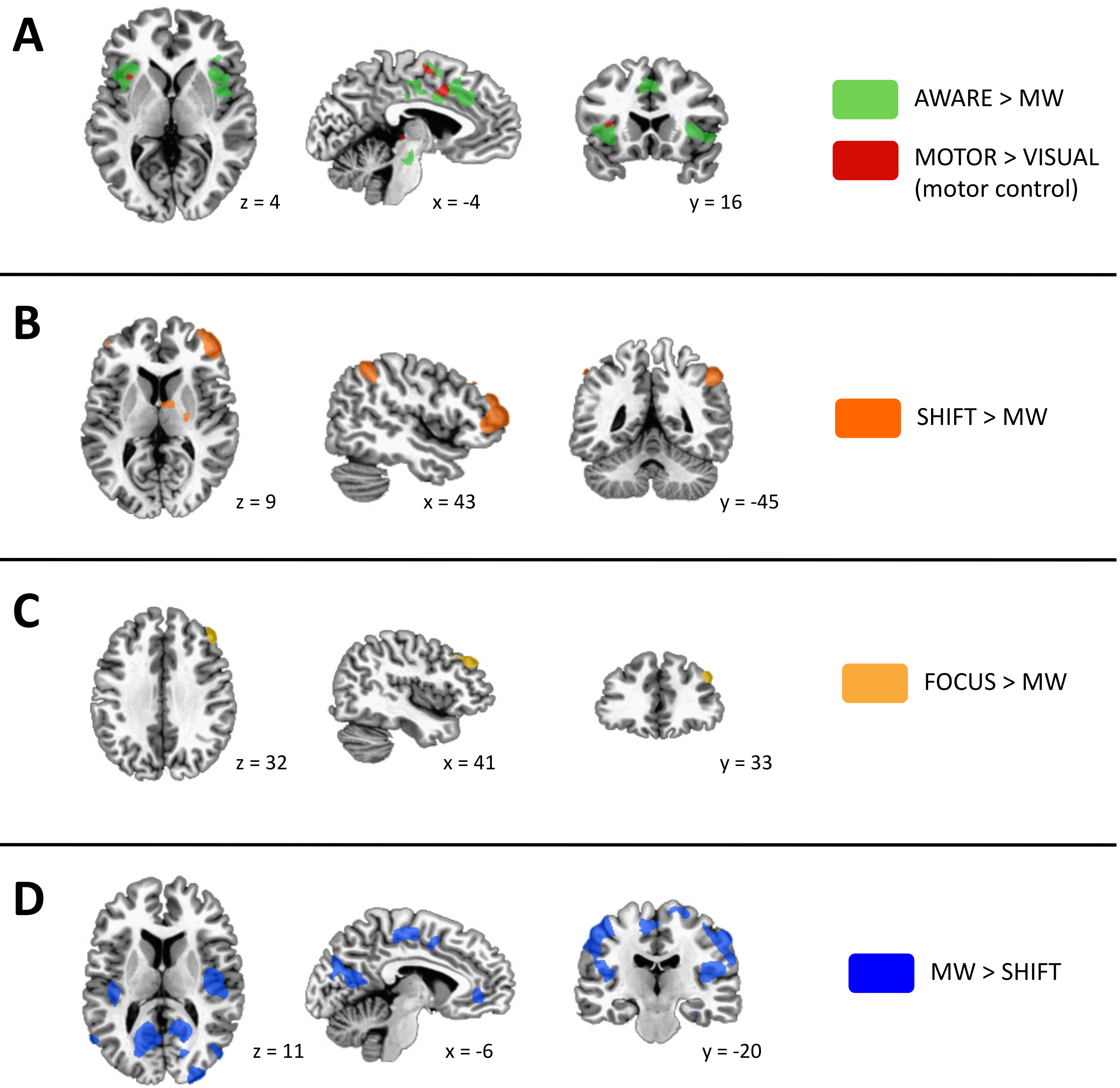
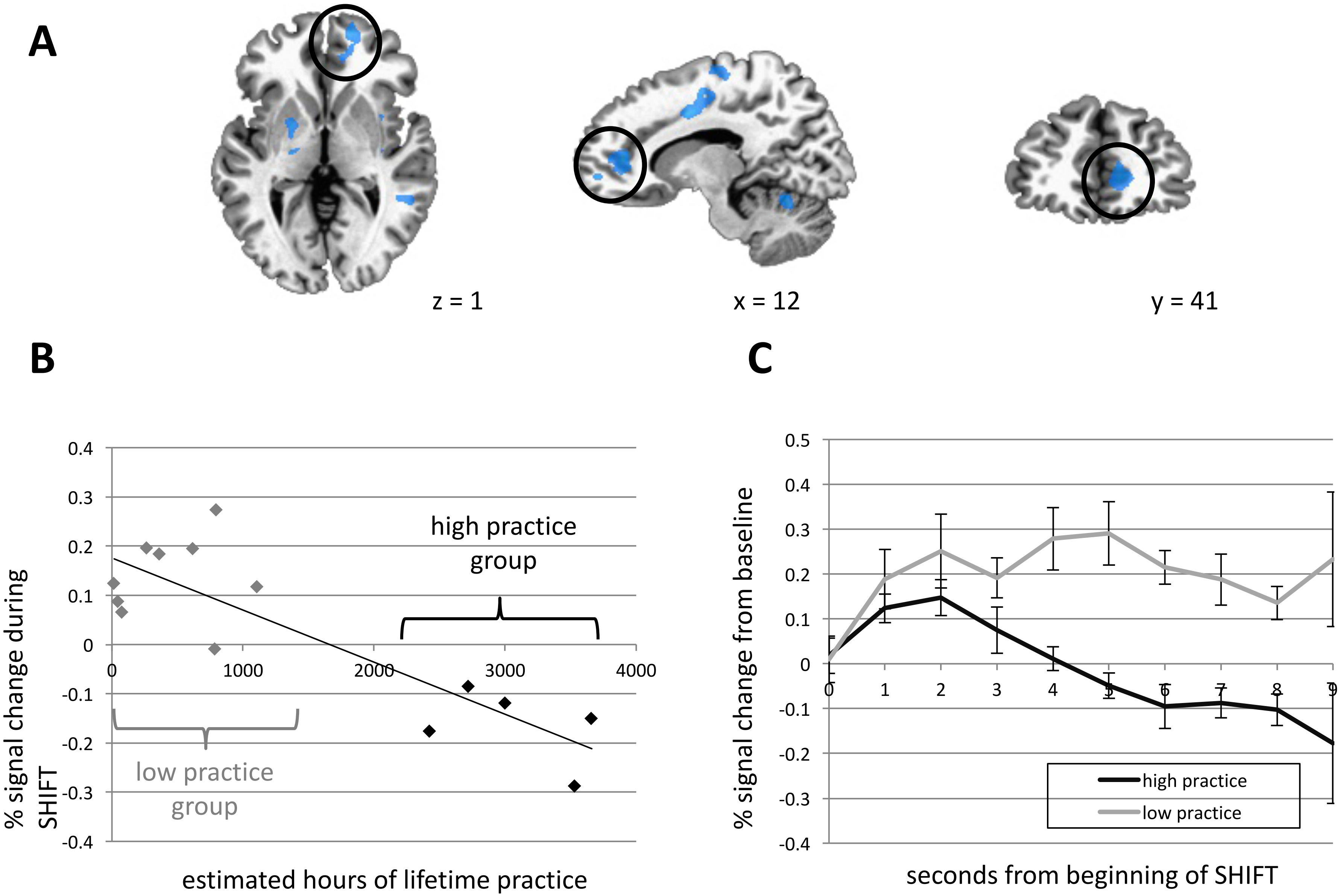

A
z = 4
x = -4
y = 16
AWARE > MW
MOTOR > VISUAL
(motor control)
B
z = 9
x = 43
y = -45
SHIFT > MW
C
z = 32
x = 41
y = 33
FOCUS > MW
D
z = 11
x = -6
y = -20
MW > SHIFT

Figure 3



A
z = 1
x = 12
y = 41
B
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0
1000
2000
3000
4000
high practice group
low practice group
% signal change during SHIFT
estimated hours of lifetime practice
C
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0
1
2
3
4
5
6
7
8
9
% signal change from baseline
high practice
low practice
seconds from beginning of SHIFT

Supplemental Materials

Materials and Methods

Participants' Meditation Background

Participants in this study had primary meditation experience in several Buddhist traditions (Shamatha/breath-focus, Vipassana/ insight, and other Tibetan styles such as compassion and tong-len). Several subjects had experience in multiple traditions, as is common with Western lay practitioners. Of the 14 total subjects, 6 primarily practiced Shamatha, 5 practiced other Tibetan styles (compassion, tong-len), and 3 practiced Vipassana. Importantly, all of these styles are built on or incorporate breath-focus meditation. Thus, all participants were very familiar with the cognitive experiences of focused attention and mind wandering, and the shifts between them, that occur during breath-focus meditation.

Motor Control Task

To account for activations due solely to motor activation from pressing a button during the meditation task, a motor control task was also performed. In each block, a dot was presented on a screen at pseudo-random intervals, six times over 21 seconds. Ten blocks were presented, with alternating instructions to either press (motor condition) or not press (visual condition) the button whenever a dot appeared. Activations during these conditions were calculated using a GLM (described in the Methods section). For each individual, activations during visual-only blocks were subtracted from activations during motor control blocks to yield an activation map representing the button press. A conjunction analysis was performed between the activation maps from this task and the AWARE condition (which included the button press) to aid in the interpretation of those results. As this task was intended as a gross functional localizer for motor activations, it should be noted that neural activations and cognitive operations in this task may differ slightly from those during the meditation task. In Figure 2a, green voxels were activated during the AWARE condition alone; voxels that were also activated during the motor control task are shown in red.

Functional MRI Data Acquisition and Pre-Processing

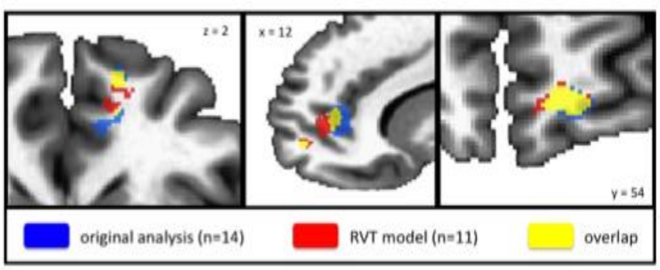
BOLD fMRI scanning was performed on a Siemens 3T MRI scanner, using a Siemens 12-channel head coil and parallel imaging with an iPAT acceleration factor of 2. Head movement was minimized with foam padding around the head. Functional images were obtained using a T2* weighted gradient-echo pulse sequence (TR=1500 msec, TE=30 msec, flip angle=90 deg, FOV=192 cm, 64 x 64 matrix, voxel dimensions=3 x 3 x 4 mm^3), providing whole brain coverage in 18 slices. High-resolution anatomical T1-weighted images were acquired for localization of task-related neural activations (TR=2600 msec, TE=3.9 msec, TI=900 msec, FOV=24 cm, 256 x 256 matrix, voxel dimensions = 1 x 1 x 1 mm^3). Respiration data were collected during scanning using a physiological monitor (In Vivo Research, Orlando, FL) connected to a dedicated computer through a data acquisition board. These data were usable for 11 out of 14 subjects (three subjects' data were unusable due to technical problems).

Initial preprocessing steps of the functional data included slice time correction and motion correction, in which all volumes were registered spatially to the 20^{th} volume in the functional run. The functional data were next smoothed using an isotropic 8 mm full-width half-maximum Gaussian kernel. Finally, the signal intensities in each volume were divided by the mean signal value for the respective run and multiplied by 100 to produce percent signal change from the run mean. All later analyses were performed on these percent signal change data. The anatomical scan was corrected for image intensity non-uniformity, skull-stripped, and then aligned with the functional data. The resulting aligned anatomical dataset was warped to Talairach space using an automated procedure employing the TT_N27 template.

Respiration Analysis

As previous work has found that meditation experience can be correlated with respiration rate (Lazar et al., 2005), we analyzed respiration in several ways in this sample. Respiration rate (breaths/minute) was calculated for each subject during the meditation task, both in the practice session and in the fMRI session. Pearson correlations were then performed between respiration rate and hours of practice. In addition, respiration rate was compared between high and low practice groups using *t*-tests, with alpha set at 0.05.

Respiration can also produce fMRI artifact, particularly in midline areas (Birn et al., 2008). To investigate this possibility, for the 11 subjects with usable respiration data, we calculated nine time-shifted respiration volume per time (RVT) regressors in a manner similar to that described by Birn et al. (Birn et al, 2006). These regressors reflect changes in the rate of breathing, and the time shifted versions of RVT changes allow for variability in the latency, from -20 s to 20 s in 5 s increments. GLMs were run for each subject including the nine RVT regressors, and the resulting betas were used in group analyses and correlations as described in the Methods section. Results from these analyses were extremely similar to those from the main analysis. Supplemental Figure 1 shows an overlay of the results in the vmPFC cluster that was significantly correlated with practice time in Figure 3, both from the original analysis and using the RVT regressors with 11 subjects.

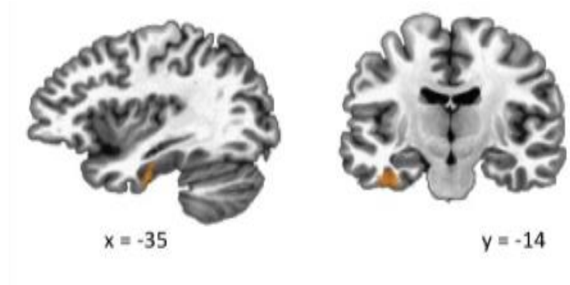


Supplemental Figure 1. Analysis of respiration effects. Overlay of vmPFC cluster examined in Figure 3, using the results of two different analyses. Blue voxels were significantly correlated with practice time in the original analysis (n=14), without controlling for possible respiration fMRI artifact. Red voxels were significantly correlated after regressing out respiration (n=11). Yellow voxels were significant in both analyses. In general, respiration had little effect on these findings.

Discussion

Practice Time Effects: AWARE

During the AWARE condition, a cluster within the left inferior temporal lobe was positively associated with practice time (Table 2), meaning that participants with more meditation experience had higher activity in this region when they became aware of mind wandering.



Supplemental Figure 2. Inferior temporal lobe cluster that was positively correlated with practice time during the AWARE condition. Subjects with more meditation experience tended to have more activity in this region when becoming aware of mind wandering.

This finding is intriguing in light of several recent reports of increased grey matter volume in this region for meditators (Hölzel et al., 2008; Luders et al., 2009). A comparison of coordinates between studies reveals a nearly precise overlap across clusters, lending weight to the suggestion that this region may be of particular importance for meditation. In one study, grey matter volume in this region was positively correlated with meditation experience (Hölzel et al., 2008). Incorporating the knowledge that activity in this region was dependent on practice time specifically during the AWARE condition, it may be that the left inferior temporal lobe is involved in the process of becoming aware of ongoing internal mentation (e.g., mind wandering in the present study). This kind of awareness is one of the main cognitive abilities that many styles of meditation aim to increase (Lutz et al., 2008).