The mind of the meditator: the influence of focused attention meditation on subsystems of the default network implicated in mind wandering

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Laymen’s summary

About 10 years ago there was a new brain network discovered completely unexpected. The discovery of this network was a fortunate accident when researchers compared the activity of the brain during a task in the (functional MRI) scanner with activity of the brain when persons lied at rest in the scanner. Particular regions in the brain spontaneously increased their activity together during rest and decreased activity when participants performed a certain task in de scanner. At first it was ignored, but later researchers started to look into this surprising activity. This was the start of a big debate in the field of Neuroscience. How is it possible that a brain at rest, without an explicit task, is so active? What could it possibly be doing? This network is called default mode network (referring to a standard mode of the brain). Recent studies have found not one default network, but three distinct default networks, referred to as subsystems. Researchers think that these individual subsystems play a different role in daydreaming (mind wandering). Mind wandering is the term for the thoughts a person has when not performing a specific task that requires attention but just let his or hers thoughts stray. You are normally not conscious of these thoughts, as this inner chatter goes on in your head almost the whole day. This article will discuss the literature in order to see how these different default network subsystems relate to specific processes of mind wandering. This review will also look into the literature about mind wandering and meditation. The practice of meditation (sitting still observing one’s own mind) seems to influence the thoughts you have when daydreaming. Researchers also investigated the brain of meditators to see which brain areas become active during meditation. Experienced meditators are masters in observing their own thoughts. This review will look if the brain regions that become active in meditators are the same regions of the default network subsystems. This is very important as it might provide new insight into methods of mental training that can enhance human wellbeing.

Introduction

A decade ago the default network was first defined as a large-scale brain system that is active during passive moments of rest opposed to during performance of externally oriented tasks (Raichle, 2001). Normally increased brain activity is thought to be associated with particular cognitive processes. Therefore the function of the default network, which is active during no particular task, has been hotly debated. Growing evidence suggest that the default mode network is involved *mind wandering,* which is defined as self generated, internally focused thoughts and feelings (Andrews-Hanna et al., 2014). Specific subcomponents of mind wandering seem to be processed by three distinct default mode network subsystems. Early studies defined the default network as one homogenous network that comprised nodes along the anterior and posterior midline, including the *medial prefrontal cortex* and the *posterior parietal cortex*. However, recent evidence pinpointed that the default network is a heterogeneous system that comprises multiple (interacting) subsystems. Andrews-Hanna and colleagues (2012; 2014) conducted an analysis (of analyses) of intrinsic activity and found a functional-anatomic fractionation of the brain's default network. Their studies revealed a *midline core* (posterior cingulate cortex and medial prefrontal cortex) and in addition, a *medial temporal lobe* subsystem and a *dorsal medial prefrontal cortex* subsystem (discussed in chapter 1). In chapter 2 existing evidence of why and how the mind wanders is discussed. The studies that exist do not encompass the subsystems recently discovered by Andrews-Hanna and colleagues (2012). The first aim of this literature review is to review the existing evidence of default network regions implicated in mind wandering to the three recently identified subsystems and relate the subsystems to different aspects of mind wandering. The *medial temporal* subsystem has been proposed to be involved in mind wandering in a memory-based simulation of past and future experiences. For example, when imaging oneself in future situations, planning upcoming activities or remembering a past experience. The dorsal medial system is suggested to be involved in introspection of mental states of self and others. The *core system* is suggested be implicated in switching between these streams of thought and integrating relevant information of both subsystems into an overarching meaning.

Meditation explores the nature of the mind, providing a method to study subjective mental states and consciousness. A second aim of this article is to review evidence to explore the idea that Focused Attention (FA) meditation might modulate the subsystems of the default network that are associated with mind wandering. In recent years the interest of effects of mindfulness meditation practice has been growing rapidly (Moore & Malinowski, 2009). Meditation practice has a highly introspective nature (Fox et al., 2012). The process of introspection that is involved in meditation basically involves observing one's own mind-wandering processes. Since meditators acquire expertise in introspection of mind wandering content and therefore develop a different relationship with it, meditation is an interesting topic for those who investigate the relationship of mind wandering and the default network. Chapter 3 discusses the practice of Focused Attention (FA) meditation, which can be defined as sustaining focus on a single object and redirect attention when the mind wanders away (Hasenkamp et al., 2012). In chapter 4, I will review the studies linking FA meditation to mind wandering. In chapter 5, I will investigate the relationship between mind wandering and the different subsystems of the default network. In chapter 6, the studies investigating the relationship between FA meditation and the default network will be discussed. In chapter 7, I will integrate these findings (mind wandering, meditation, default network) to review the hypothesis that effects of FA meditation on mind wandering could be linked to changes in activity of the distinct subsystems of the default network implicated in mind wandering. Finally, I will propose a future research agenda. A second aim of this article is to review evidence for the hypothesis that FA meditation modulates the subsystems of the default network that are associated with different mind wandering processes. Figure 1 displays an overview of the different components that will be reviewed. Studying the human brain when mind wandering and relate this to meditation is highly relevant as it might provide new insight into human consciousness and methods of mental training that can enhance wellbeing.

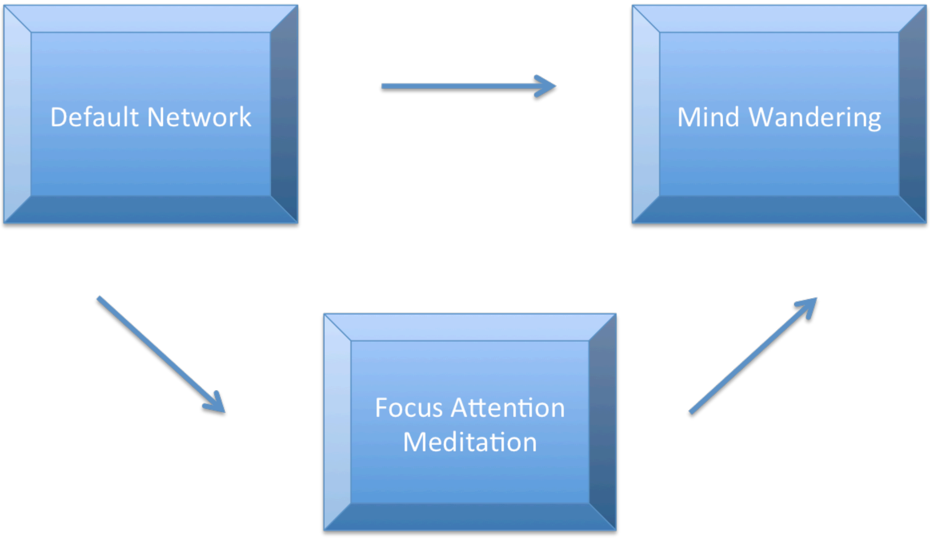

Figure 1. Overview of the three main relationships that will be reviewed; This review will describe the existing literature that investigated: the relationship between FA meditation and mind wandering (Chapter 4); the relationship between recently identified subsystems of the default network and mind wandering (chapter 5); the relationship between FA meditation and default network (chapter 6).

Chapter 1. The Default Network

One of the most intriguing findings of the past decade in human functional imaging has been the observation that particular regions of the human brain increase its activity during passive states (Buckner., 2008). This group of brain regions have collectively been defined as 'the default network'. Normally increased brain activity is thought to be associated with particular cognitive processes. Therefore, the function of the default network, which is active during no particular task, has been intensively debated. Early studies defined the default network as one homogenous network that comprised nodes along the anterior and posterior midline, including the *medial prefrontal cortex* and the *posterior parietal cortex* (Buckner., 2008). However, recent evidence pinpointed that the default network is a heterogeneous system that comprises multiple (interacting) subsystems supporting multiple component processes (Andrews-Hanna et al., 2012). Studies of intrinsic activity revealed a *midline core* (posterior cingulate cortex and medial prefrontal cortex) and extensional evidence that the default network comprised a *media temporal lobe* subsystem and a *dorsal medial prefrontal cortex* subsystem each thought to support different cognitive functions when an individual lies at rest without a current task.

1.1 Discovery of the default network

Resting-state induced deactivations: 'task-negative network '

The discovery of the default network was a fortunate accident that occurred due to the inclusion of rest control conditions in early PET & functional MRI studies (Ingvar, 1974; Raichle, 1987). The common practice of rest conditions as experimental control in *PET & functional MRI* research revealed specific brain regions that were more active during passive control states (individual lies at rest in the scanner) compared to goal directed active-tasks (individual performs a certain task in the scanner) (Buckner et al., 2008; Buckner, 2011). Regions relatively more active in the experimental condition (i.e. reading, classifying pictures) were called '*activations*' and regions less active in the experimental condition compared to the control condition were called ' *deactivations*' (Buckner et al., 2008). David Ingvar (1974) was the first to investigate imaging findings from the rest task states. He suggested that increased activity during rest is confined to specific brain regions, especially the prefrontal cortex. A commonly observed form of deactivation in later studies was along the frontal and posterior midline (see figure 1) (Buckner et al., 2008).

Establishment of the default network as brain system

Two meta-analyses that pooled extensive data provided broad awareness of the common brain regions that become active during passive task conditions. Shulman (1997) and colleagues pooled positron emission tomography (PET) data from 132 healthy adults from studies in which an active task, such as word reading and stimulus classification, could be directly compared to a passive task, in which the same visual words or pictures were shown but with no explicit task to perform. Mazoyer and colleagues (2001) used a similar approach with visually and aurally active tasks compared to rest conditions in 63 healthy adults. Both studies revealed extremely consistent brain regions that were more active during the passive task conditions (see figure 1). The most common regions were *medial frontal* (dMPFC and vMPFC) and *parietal cortical regions* (posterior cingulate cortex). Due to the the broad consistency of the resting state activity pattern across different studies, Mazoyer and colleagues (2001) hypothesized that a common set of spontaneous cognitive processes emerged in the passive-task conditions. This new focus on the 'baseline state' of the brain was important to the developing concept of a default network. Several lasting results on the study of the default network emerged. One of the main suggestions of influential papers suggested that default mode network activity might be implicated in spontaneous self-generated thought occurring during mind wandering (see chapter 2) (Mason et al., 2007). In sum, research emphasized that the default network is a fundamental neurobiological system with unique physiological and cognitive properties that is different from other systems and should be explored as own area of study. It caused many researchers to wonder about the adaptive functions of spontaneous self generated thoughts and its intrinsic neural processes.

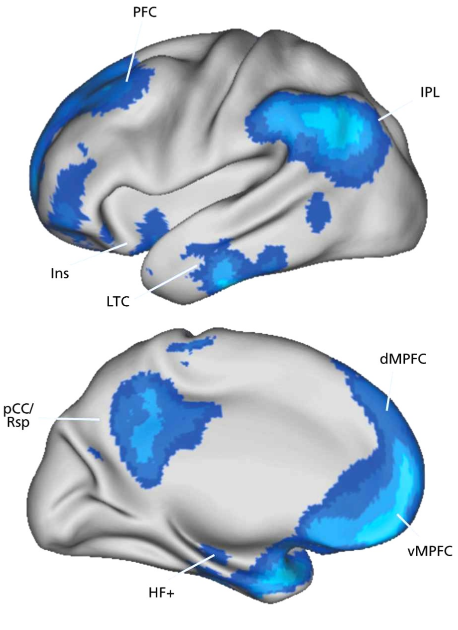

Figure 1. Default network activity of PET meta-analysis of Shulman (1997; described in Buckner et al., 2008). Most active regions in passive task states are visualized in blue.

1.2. Anatomy of the Default Network

The anatomy of the default network is identified using multiple approaches.

1. Blocked Task-Induced Deactivation

This paradigm consists of extended epochs (blocks) of active and passive tasks that are compared with one another. During these scan-epochs, activity is averaged over a block of multiple task trials. As noted earlier, Schulman et al. (1997) and Mazoyer et al. (2001) published meta-analyses to identify brain regions more active during passive tasks (see figure 1). Figure 2A shows a third meta-analysis of blocked task data. Four *fMRI* datasets of 92 participants were analysed (Shannon, 2006). The active task involved a semantic decision on presented words and the passive task a visual fixation. A consistent set of brain regions was found across all three meta-analysis studies in the passive condition. The regions included: the ventromedial prefrontal cortex, dorsal medial prefrontal cortex, the Posterior Parietal Cortex/ Retrosplenial cortex, Inferior Parietal Lobe, the lateral temporal cortex and the hippocampal formation (see figure 2A) (Schulman et al., 1997; Mazoyer et al., 2001; Shannon, 2006).

2. Event-Related Task-Induced Deactivation

Alternative to block designs are event related designs. Here, stimuli are presented randomized. Within each trial there are a number of events such as the presentation of a stimulus and the response period. This design allows one to observe the differences in neural activity associated with each event rather than blocks of multiple sequential task trials in block designs (Buckner, 1998; 2008). A reason to use an event-related design is that is it possible that extended epochs are needed to elicit activity during passive epochs. This might be the case if blocked task-induced deactivations arise from slowly evolving signals and therefore do not reflect a specific cognitive state (Buckner et al., 2008). A meta- analysis that used event related fMRI data of 49 subjects to define the anatomy of the default network is illustrated in figure 2B (Shannon, 2006). The task consisted of semantic and phonological classification. As can be seen in figure 2B, the default network that is based on event related design is highly similar to that of blocked task-induced deactivations. The additional conclusion that can be drawn from the data of the event related design is that the difference in activity of the default network between active and passive tasks can emerge fast, in less than seconds.

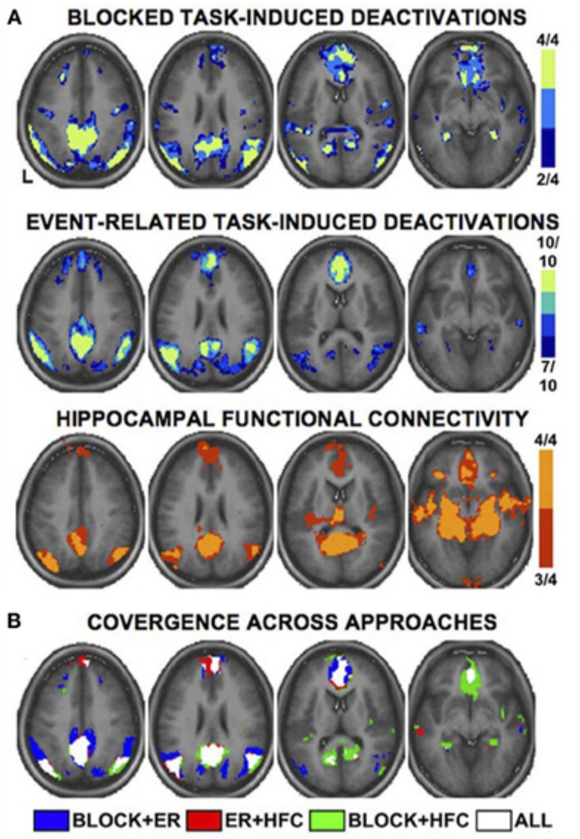

Figure 2. Default network activity defined by different fMRI approaches. (A) Each row shows a different approach as described in the text. Data is based on meta-analysis that included 4 block design fmri studies, 10 event related design fMRI studies and 4 functional connectivity studies. The maps embody a meta-analysis of multiple data sets. Colours describe number of datasets with a significant effect (scales on the right). Blue (B) Convergence across all approaches show the core regions of the default network as described in the text. Block = block related design, ER= event related design, HFC = hippocampal functional connectivity, ALL = all designs combined. Adapted from Buckner et al (2008).

3. Resting state functional connectivity

A final approach that defines the functional anatomy of the default network finds its base in measuring the brain's intrinsic activity. At all levels of the brain, there is spontaneous activity, which reflect direct and indirect anatomic connectivity (Buckner, 2008). Low-frequency spontaneous correlations are detectable with MRI. Studying intrinsic activity correlations is a valuable method to evaluate regional interactions that occur when a subject is not performing an explicit task. Several new studies defined the default network on the basis of patterns of temporal correlations using *resting state functional connectivity* (RSCF) MRI (Yeo et al., 2011; Choi et al., 2012; Buckner et al., 2011). The idea behind this method is that default network activity is anti-correlated with task-positive networks. Independent networks are uncorrelated over time. Yeo and colleagues (2011) conducted a meta-analysis of 1000 subjects where they applied clustering techniques to RSCF data. The default network included voxels covering *the medial prefrontal cortex (mPFC), the lateral frontal cortex, the medial parietal cortex, the medial temporal lobe, the lateral parietal cortex, and the lateral temporal cortex* (see table 1). Again, there is broad convergence between the anatomy of the default network defined by RCSF and large-scale meta-analyses of functional imaging data.

Core regions of the default Network in humans

There is nearly complete convergence across the datasets discussed above with the medial frontal cortex (mPFC), posterior cingulate cortex (PCC)/retrosplenial cortex (Rsp) and the inferior parietal lobe (IPL) and the hippocampal formation (HF+). These regions, The HF+, PCC, IPL, mPFC (ventral and medial), show convergence with the meta-analyses of Shulman et al. (1997). The lateral temporal cortex (LTC) is consistently shown across all approaches, only less strong. Taken together, these observed regions define the core anatomical regions of the default network (see table 1).

1.3. Multiple interacting subsystems

The default network seem to consist of a set of brain regions that are co-activated during non-task states and show intrinsic functional correlation with one another. Therefore early studies characterized the default network as a homogenous network (Uddin et al., 2009; Greicius et al., 2003). The default network is thought to play an important role in self-generated thought (autobiographical memory, future thinking, theory of mind, self-referential processing etc). The complexity of these experiences suggested that different components of the default network might contribute to different aspects of self-generated thought. Andrews-Hanna and colleagues (2010) were the first to test this hypothesis and found the first evidence for the idea of different subsystems within the default network. They used hierarchical clustering analyses to analyse data from *resting state functional connectivity* and *task-related fMRI*. Data of eleven brain areas of the default network were divided into two separable components. The first component, a *medial temporal subsystem*, consisted the hippocampal formation (HF+), parahippocampal cortex (PHC), the retrosplenial cortex (RSC), the posterior inferior parietal lobe (IPL) and the ventromedial prefrontal cortex (vmPFC). The second component, a *dorsal medial subsystem*, consisted of the dorsal medial PFC (dmPFC), the temporoparietal junction (TPJ), the lateral temporal cortex, and the temporal pole (TempP) (Andrews-Hanna et al., 2010). Both components were highly correlated with a midline core (core subsystem) consisting of the anterior medial prefrontal cortex (amPFC) and the posterior cingulate cortex (PCC). Interestingly, this analysis yielded new regions of the default network, namely the *TPJ, amPFC, TempP*, and the *PHC*,

These findings have extensively been replicated. Yeo (2011), Buckner (2011) Choi (2012) and colleagues applied clustering algorithms to resting-state activity from 1000 subjects, which subdived the default network into the same subsystems similar to the study of Andrews-Hanna et al. (2010). Default network components of the clustering algorithms to resting state activity of Yeo (2011), Buckner (2011) and Choi (2012) are broadly consistent with the hierarchical clustering analysis of Andrews-Hanna et al. (2010). However, there were also important differences found between the two different analyses. The dorsal medial subsystem was left lateralized in the study of Yeo et al. (2011) and contained lateral prefrontal regions such as the *lateral superior frontal cortex*, *ventrolateral PFC* and the *inferior frontal gyrus*, Furthermore, the amPFC - PCC core system they uncovered had additional regions in the superior part of the *angular gyrus* (Yeo et al., 2011).

What is clear is that new techniques revealed that the default network appears to be a heterogeneous brain network that encompasses at least three separable components: a dorsal medial subsystem, a medial temporal subsystem and a core system.

Table 1. Areas of the default network as described in text

	Functional MRI Meta analyses (Buckner et al., 2008) *	**Dorsal Medial Subsystem (Andrews-Hanna et al., 2014) ***	**Medial Temporal subsystem (Andrews-Hanna et al., 2014) ***	**Core Subsystem (Buckner et al., 2008; Andrews-Hanna et al., 2014) ***
Region	vMPFC		vMPFC	aMPFC
	PCC/Rsp	*TemP*	Rsp	PCC
	IPL	*TPJ*	IPL	
	LTC	LTC		
	dMPFC	dmPFC		
	HF+		HF+	

Notes: Labels are in correspondence with the areas in humans described by Brodmann. Abbreviations are described in text. HF+ includes parahippocampal cortex (PHC). Italic regions are regions first described in Andrews-Hanna et al., (2010) others are convergent across Meta analyses.

The first evidence of the functional dissociation within the default network was provided by Yarkoni and colleagues (2011). They conducted an influential fMRI meta-analysis to decode the functional properties of the three default network subsystems. Episodic processes such as autobiographical memory and episodic future thought are correlated with the *medial temporal subsystem*. *The dorsal medial subsystem* is engaged by metacognitive thoughts, such as mentalizing and theory of mind. Andrews-Hanna (2014) proposed that this subsystem might support meta-cognitive aspects of internally guided cognition, allowing us to reflect upon our own and others mental state. The medial temporal lobe subsystem is thought to facilitate construction of imagined scenes based on memory. The core subsystem is hypothesized to be an important zone of integration between the two subsystems. It is thought to asses personal relevance of incoming information, allowing an individual to integrate current mental states with prior conceptual and episodic knowledge into an overarching personal meaning.

Table 2. Two categories of mind wandering thought content underpinned by dissociate subsystems of the default network (adapted from O' Callaghan et al., 2015)

Dorsal Medial prefrontal subsystem *Introspection/meta cognitive*	**Medial temporal lobe subsystem** *Memory based construction/simulation*
Personal semantics	Episodic/autobiographical memory
Appraisal of own mental state	Episodic future thinking
Social Reasoning	Prospective memory/planning
Metacognition	Scene construction/navigation
Self-referential statements	Contextual associations
Appraisal of other's mental state	Semantic/conceptual associations
Thought/concern for others	Imagery/imagination

1.4. Conclusion

The last years there has been an increase in studies describing properties of the default network with different (imaging) techniques and approaches. Recent analysis of intrinsic functional correlations between brain regions in humans suggest that the default network is not a homogenous network consisting of midline regions but rather is organized as a set of interacting subsystems, including a medial temporal, a dorsal medial subsystem and a core system. The default network is not a passive network as recent evidence suggests. It appears to contribute to several active forms of internally directed cognition that will be discussed in chapter 2.

Chapter 2. Mind wandering

The spontaneous activity in a set of brain regions when people lie at rest passively thinking to themselves in a PET or MRI scanner is one of the most unexpected findings by functional neuroimaging. This emerging observation elicited a debate about its function and questions about its adaptive role for cognition. Converging evidence links the default network to spontaneous, self- generative thought- referred to as *mind wandering* (Smallwood & Schooler, 2014). We spend approximately half our waking day engaged in mind wandering (Killingsworth & Gilbert, 2010). Such internal mentation can exert important consequences to our emotional wellbeing, self-reflection, planning, social emotional processing and decision-making (O' Callaghan et al., 2014). Mind wandering has been associated with regions of the default network. In this chapter we explore what mind wandering is, how it can be assed in an experimental setting, its phenomenology, different types of mind wandering content and theories about mind wandering.

2.1. Terminology: What is mind wandering?

When the mind wanders, attention shifts away from a current (external) task to mental content generated by the individual itself opposed to cued by the environment (Smallwood & Schooler, 2014). The experience of mind wandering is described with varying terminology. For instance, the thoughts that appear during mind wandering are described as *task unrelated thoughts*[1] (Giambra, 1989) *stimulus independent thoughts* (Antrobus et al., 1966) autobiographical thought (Kvavilashvili & Mandler, 2004). Self- generated thought is a much-used term that is linked to the content of mind wandering. It describes both the indepence from perception as well as the generative aspects of mind wandering (Smallwood & Schooler, 2014). The term self-generated thought emphasizes that it arises not from extrinsic changes in the environment, but rather arises from intrinsic changes that appear within an individual (Smallwood & Schooler, 2014). However, the term self-generated thought is not specific to states of mind wandering. It describes the processes that are involved in generating mental contents that are not primarily driven by the external environment. Whilst mind wandering is thought to occur always in relation to a current task, self-generated thought also occurs in the absence of a task (e.g. day dreaming).

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[1] See section '*self-generated thougt'* for a critical nuance of this allegation

It is important to keep in mind that mind-wandering thoughts can be task related as well as task unrelated. For example, when writing a scientific article thoughts about what journal to send your manuscript to are task related. But when driving an automobile and thinking about what dress to wear for an upcoming party is a form of mind wandering unrelated to the task. This distinction of mind wandering thoughts from the term task-relatedness is important. Earlier studies linked mind wandering to task-unrelated passive states, however recent studies emphasize that episodes of mind wandering are not limited to task-unrelated thoughts but might also contain task related self-generated thoughts (Smallwood & Schooler, 2014).

2.2. Measurement of mind wandering

The first choice technique of measuring the frequency and content of mind wandering is Experience Sampling (ES). Experience sampling is a method in which subjects are intermittently probed about their current mental state. It is a methodology based on self-report of the participant. This measurement corresponds to the content of conscious experience at particular moments in time. There are different methods of ES:

1. Probe-caught method

Subjects are intermittently interrupted and probed about the content of their experience. These appear in a random way. This method allows an assessment of the amount of mind wandering that is occurring. The experimenter is able to objectively quantify the relative amount of mind wandering that the individual is aware of.

2. Self-caught method

Subjects are asked to report when they catch their mind wandering. This provides a straightforward assessment of the number of mind wandering episodes that reached the awareness of the subject. A disadvantage of this method is that subjects must be meta-conscious of the mind-wandering episode in order to report it.

3. Retrospective method

ES data is gathered at the end of a task via questionnaires. An advantage of this method is that it preserves the natural time course of the task. This can be important in resting state fMRI. A disadvantage of this method is that subjects need to recall mind-wandering episodes, therefore may cause a recall bias (also known as response bias).

4. Open ended method

Subjects are asked to describe with their own words what they experienced during a task. The advantage of this method is that there are no categories imposed that can constrain reports of the subjects. A disadvantage of this method is that can be difficult to compare the meaning of responses because it allows subjects to use their own words.

Conceptual issues of measuring mind wandering

Mind wandering episodes depend for a large extent on processes that are spontaneous instead of induced directly by an experimenter (Smallwood & Schooler, 2014). Therefore there are at least three important conceptual issues that arise in the investigation of mind wandering.

1. *Absence of direct experimental contro*l. Research lacks the ability to directly cause the mind to wander.
2. *The covert nature of self-generated thoughts*. They are fundamentally internal, with few external manifestations. Therefore, it cannot be independently verified.
3. *The validity of introspective evidence by experience sampling*. Self-report introspection is subjective and therefore has limited validity. Furthermore, they are difficult to verify objectively.

Although ES is a valuable method to study mind wandering, it also has the risk that reporting on introspection changes the nature of the state that is being assessed (Smallwood & Schooler, 2014). Furthermore, a big disadvantageous of this methodology is that Experimental Sampling (ES) does not enable experimenters to investigate in real time the mind wandering state evolving from one mental state to the next. For this reason, it is important that indirect measures of mind wandering experiences must be pursued and will be discussed below

Indirect behavioural measures of mind wandering

It is common to study cognitive functions trough manipulation of its underlying process. By varying the nature of the stimulus or task that subjects perform and subsequently observing changes that occur due to these variation, you can draw inferences about the nature of the underlying mental process. Manipulating mind wandering to gain experimental control and allow the identification of causal relationships can be achieved in several ways. A first way to manipulate mind wandering is trough the induction of psychological states that alter the occurrence of mind wandering or the mental content of mind wandering states. The induction of negative affect (Smallwood et al., 2009a; Smallwood & O' Connor., 2011) alcohol intoxication (Sayette et al., 2010) and craving (Sayette et al., 2012) are linked to an increase in mind wandering.

Another way is to modulate the complexity of the demands of the task that participants perform. This is thought to change the amount of time that subjects engage in task-unrelated thoughts. It is thought that a relatively boring task wit low task demands causes greater mind wandering and demanding tasks causes more sustained attention and less mind wandering. A much-used task is a reading comprehension task.

Another behavioural measure to indirectly study mind wandering is a Sustained Attention Response task (Go/No Go task). The Sustained Attention Test is a computer-based task designed to measure a person's ability to withhold responses to infrequent and unpredictable stimuli during a period of rapid and rhythmic responding to frequent stimuli.

A common approach is to vary between a choice reaction time task and a working memory task (Smallwood et al., 2009b). Here, perceptual input is constant. Yet, the working memory task requires participants to continually encode and maintain this stimulus, while this is not necessary in the choice reaction time task. As a result, there is more task unrelated thought in the choice reaction time task. Studies have found that variability of response time is characteristic of the mind wandering state (Carriere et al., 2008; Cheyne et al., 2006, 2011) with a longer response time indicating more mind wandering. In behavioural measures of mind wandering, it is thought that mind wandering is reflected by impaired task accuracy, increased reaction time and response variability. (Mooneyham & Schooler, 2013).

2.3. Phenomenology

Research over the past decade has explored different aspects (form/content) of mind wandering (Smallwood & Schooler, 2014).

Content of self-generated thought

Studies show that mind wandering thoughts often are a dynamic mix of thoughts regarding the future and memories from the past that have personal relevance to the individual (Smallwood & Schooler 2014, Andrews-Hanna, Smallwood & Spreng, 2014). Despite the varied mixture of thoughts that occupy our minds when mind wandering, research exploring the content of mind wandering has found a number of general principles that explain this complex mixture. The content of self-generated thoughts during mind wandering can be explained by three components: 1) temporal focus (past/future), 2) affective state of the individual (negative/positive emotional valence) and 3) interest (self/other) (see figure 3).

1. Temporal focus

A study of Baird et al. (2011) used open ended ES and found that there is a *bias* towards thinking about the future. 48% of time participants engaged in thinking about the future, 29% in thinking about the present and 12% thinking about the past. 11% of the time subjects reported to have no temporal focus (see figure 3a). Studies have defined the bias towards thinking about the future as *the prospective bias* (Smallwood & Schooler, 2014). Furthermore, a *retrospective bias* (a bias towards thinking about the past) is correlated with low mood. Unhappiness is correlated with mind wandering in general, but particularly pronounced for mind wandering episodes focused on the past (Smallwood et al., 2004) Studies reported that mind wandering about the past and future has distinct psychological correlates (see figure 3b) (Smallwood et al., 2009a).

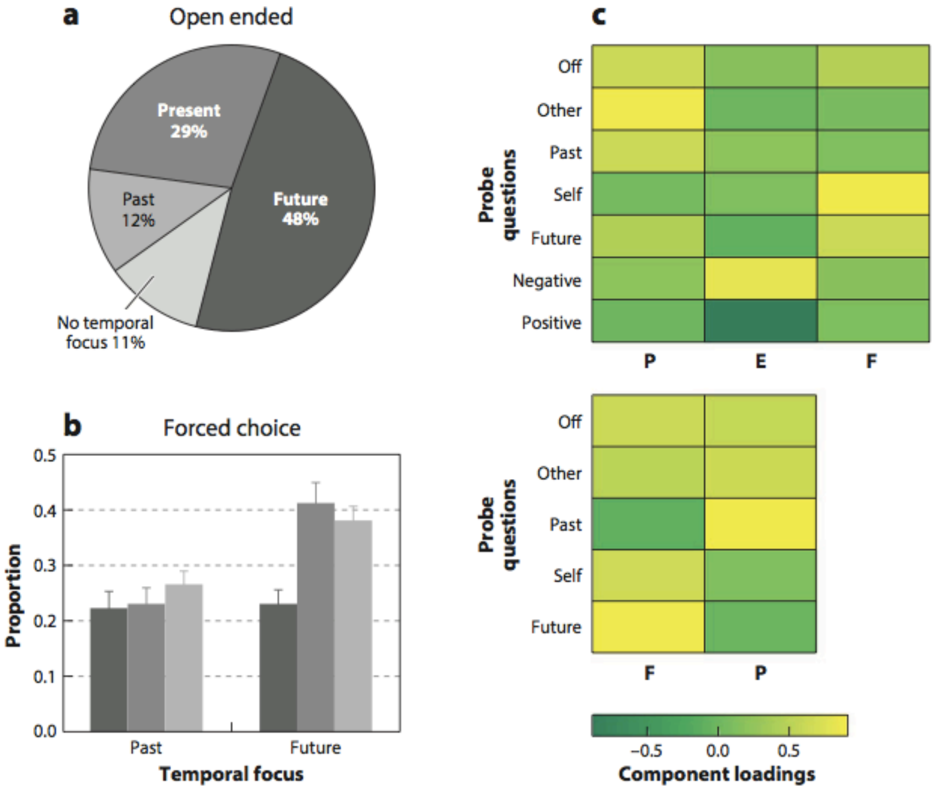


Figure 3. Content of thoughts during mind wandering states: a) A study of Baird et al. (2011) used open-ended ES and found that there is a prospective bias to the thoughts subject experience during mind wandering. b) A study of Smallwood et al. (2009a) using forced choice ES found that the prospective bias is reduced in a task that requires working memory (dark grey bar) compared to relative less cognitive demanding tasks such as choice reaction time task (middle bar) and passive viewing (light grey bar) c) PCA analysis of Ruby et al. (2013a,b) which shows that mind wandering thoughts have different categories of experience that can be distinguished based upon their focus on the Past (P), Future (F) and Emotion (E).

2. Affective state

An experience-sampling study conducted on large scale found that when people mind wander their mood is generally low (Killingsowrth & Gilbert, 2010). Recent evidence has found that this relationship is mediated by the content of the mind-wandering thoughts. Thoughts about the past indicated higher levels of unhappiness (Poerio et al., 2013, Stawarczyk et al. 2013, Smallwood & Schooler, 2014); while future thinking tends to reduce negative mood (Ruby et al. 2013a). These findings implicate that affective processes might have an important influence on the content of self-generated thought during mind wandering.

3. Temporal Focus, Valence & Interest

A way to investigate the wide variety of experiences during mind wandering states is exploring the patterns of covariance in ES data. In order to do this, multiple dimensions of ES data are collected at the same time and decomposed with statistical analysis. Ruby and colleagues (2013a) conducted a principle component analysis (figure 3c) to decompose the content of task unrelated thought during a simple non-demanding laboratory task. This revealed that self-generated thoughts consist of two different components of social thought; Thought related to the past and thoughts related to the future. A third component that was identified was: emotional valence (negative/positive). A last component was the variable interest (self/other). The PCA to ES data confirmed that these components are unique statistical categories of thought. Positive weighting of the different elements of experience are reflected in warm yellow and a negative weighting is described in cooler green in figure 3c.

Meta awareness

Research has focused on the relationship between mind wandering and meta-awareness. Meta awareness is the explicit awareness of an individual of their current content of thoughts (Smallwood & Schooler, 2014; Schooler et al., 2011). An important feature of mind wandering is the point at which we recognize that the current content of thought is wandered away from the task that the individual is performing. Mind wandering reflects in certain occasions a failure to maintain conscious awareness on the links between the content of conscious thought and our current goals. There are two approaches to investigate meta-awareness of mind wandering namely the probe caught and self caught method. In the probe caught paradigm subject are asked to indicate whether they had been aware that their minds had wandered. The self-caught paradigm is able to investigate how effectively subjects notice that their minds have wandered. These self-caught reports are thought to represent mind wandering episodes that reached meta-awareness. By comparing self caught mind wandering with probe caught mind wandering episodes it is possible to inference about the role of meta-awareness in various situations where mind wandering occurs.

2.4. Theories about mind wandering

Perceptual decoupling

When attention is directed to an external task or goal, it can facilitate action by increasing the processing of relevant sensory input (Posner & Peterson, 1990). Oppositely, when mind wandering occurs it becomes disengaged from the external world. This shift in attention is known as *perceptual decoupling*. Perceptual decoupling/coupling is the capacity for the mind to flexibly disengage and engage attentional processes from sensory input (Smallwood & Schooled, 2014). Evidence for perceptual decoupling is found in studies that explore the temporal relationship between self-generated thought and the cortical processing of external information. The amplitude of an evoked response to a stimulus (known as Event related potentials (ERP's) are a way of quantifying the cortical processing of external information (Smallwood & Schooler, 2014). More specifically, an ERP known as the P3 follows 300 ms after task relevant events are processed. The P3 reflects task relevant attention (Polich, 1986). Evidence of the decoupling of attention from perception during the mind wandering state is derived from two representative studies examining the amplitude of evoked response during processing of events in a task (Barron et al., 2011; Kam et al., 2011; Smallwood, 2011b). These studies showed that the amplitude of the P3 is reduced in subjects engaged in task-unrelated thought (Barron et al. 2011; Kam et al., 2011). A study manipulated the occurrence of task unrelated thought and investigated whether this was associated with a reduction in the amplitude of the ERP P3. Smallwood and colleagues (2011b) designed an experiment in which subjects were engaged in a choice reaction time task that required no external attention during a no-response period, and a working memory task that required continuous attention during the no response period (Smallwood, 2011b, figure 4c). Evoked neural responses can be measured by evoked changes pupil dilation. The results of this study showed that pupil signal shows greater evoked response during the working memory task (see figure 4d, in red) than during the choice reaction time task (see figure 4d, blue line). Indicating that periods requiring external task focus were characterized by large task-evoked changes in pupil dilation. In sum, the occurrence of mind wandering and the conditions that promote it are associated with a reduced evoked response to external events known as perceptual decoupling.

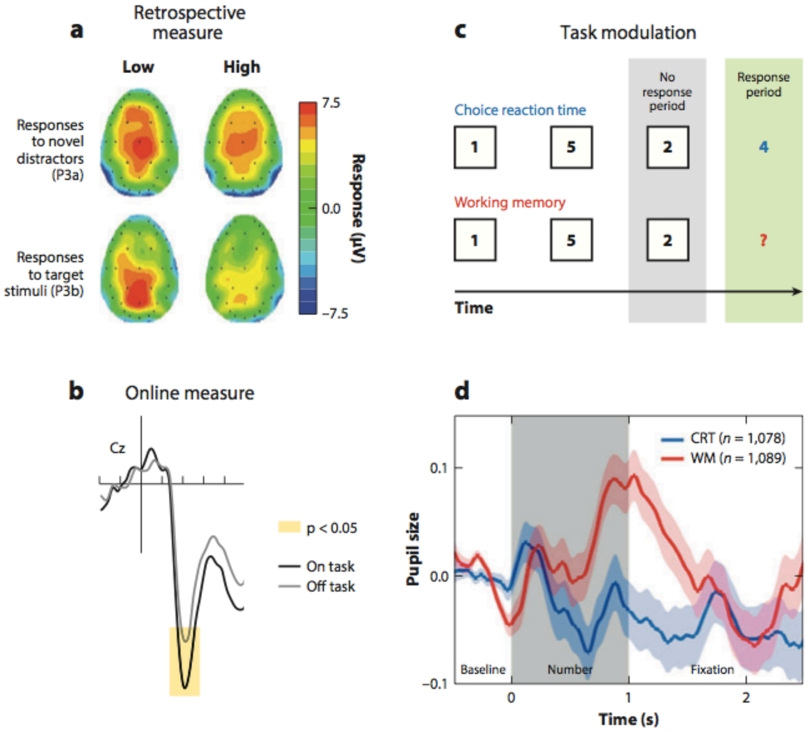


Figure 4. Key results demonstrating perceptual decoupling of attention form perception. A) Barron et al. (2011) b) Kam et al. (2011) c) Smallwood (2011b)

Wanted vs. unwanted mind wandering

Mind wandering can be experienced as either wanted or unwanted (Kane & McKay., 2012). Mind wandering can be useful by providing mental breaks to relieve boredom tasks. Another beneficial outcome of mind wandering is the capacity to generate novel and creative thoughts. Unwanted mind wandering is associated with rumination and unwanted intrusive thoughts. And has been linked to poor outcomes in a range of tasks (Smallwood & Schooler, 2014).

2.5. Conclusion

A major upsurge in mind wandering research over the past years has increased our understanding of its frequency, content, theories and context. Overcoming challenges in the quantification of mind wandering resulting from the dependence on self-report, lack of direct experimental control and the hidden nature of mind wandering is important. The content of mind wandering thoughts can differ regarding the temporal focus (past/future), affective state (negative/positive) and interest (self/other). Attention is engaged from external input during mind wandering. Mind wandering has both benefits when wanted, and costs when unwanted. A way to gain insight in mind wandering processes is mindfulness meditation and will be discussed in the next chapter.

Chapter 3. Mindfulness & Meditation

Research into both mindfulness and mind wandering has grown rapidly the past years. However, very few studies have directly connected the two. Mindfulness is a core element of diverse forms of meditation. When in meditation, people spend a lot of time observing their minds. Therefore, mindfulness might help us understand how mind wandering work. This chapter will explain what mindfulness and meditation is. It will discuss the two general forms of meditation practice. According to popular literature mindfulness is theoretically the opposite of mind wandering. But what is the evidence for this inference? I will reflect on the idea of mindfulness being the opposite of mind wandering.

3.1. Mindfulness

Mindfulness is a psychological state in which full attention to experiences of the present moment without emotional reactivity and conceptual elaboration is maintained (Bishop et al., 2004). It is also described as the dispassionate, non-evaluative moment-to-moment awareness of thoughts, emotions, perceptions and sensations (Marchand, 2014). Mindfulness is most commonly defined as the state of being attentive to and aware of what is taking place in the present, in short referred to as *present moment awareness* (Levinson et al., 2014). The concept of mindfulness has roots in Buddhist and other contemplative traditions where conscious attention and awareness are actively cultivated (Brown & Ryan, 2003). Nyanaponika Thera (1972), a therevada monk, described mindfulness as "*the clear and single minded awareness of what actually happens to us and in us at the successive moments of perception*". Hanh (1976), a renowned Vietnamese Zen-Buddhist monk, defined mindfulness as " *keeping one's consciousness alive to the present reality*". Mindfulness training involves meditation. Meditation has two components: maintaining attention on the immediate experience and maintaining an attitude of acceptance towards this experience (Bishop 2004). Mindfulness meditation practice is the framework that is used to develop the state of mindfulness.

3.2. Meditation

The word meditation is derived from the Latin word *meditari*, which means 'to participate in contemplation or deliberation.'(Marchand, 2014). Meditation can be conceptualized as a family of complex emotional and attentional regulatory training developed for different goals, including the improvement of wellbeing and emotional balance (Lutz et al. 2008). Two general forms of meditation have been distinguished in the scientific literature: *focused attention* and *open monitoring* (Lutz et al., 2008).

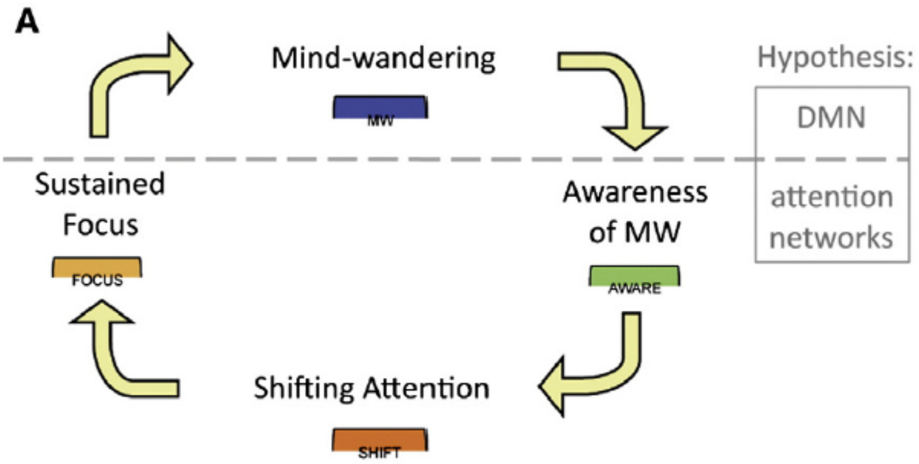


Figure 5. Theoretical model of the cycle of four phases (mind wandering, awareness, shifting attention and sustained focus) during Focused Attention Meditation of Hasenkamp et al. (2012).

Focused Attention meditation

During FA practice the meditator attempts to maintain focus on a particular object (e.g. the breath) (Hasenkamp et al., 2011). The meditator must constantly monitor the quality of attention to maintain the focus on the object of attention. When attempting to sustain focus on an object such as the breath, one inevitably experiences mind wandering. At a certain point during mind wandering the practitioner becomes aware that the mind is not focused on the object. At that point he/she disengages from the train of thought and shifts attention back to the object, where it stays focused again for some period of time until the mind starts wandering again and the cycle repeats. Figure 5 shows a model with the attentional cycle during FA practice. This cyclical process is repeated throughout a session of FA meditation (Hasenkamp et al., 2011). This practice is thought to develop three skills that regulate attention (Lutz et al., 2008). The first skill is the capacity to remain vigilant to distractors. The second skill is the ability to disengage from a distractor. The last skill is the ability to redirect the focus back to the chosen object. Advanced meditators have the ability to acute notice when the mind has wandered (Lutz et al., 2008). Thus, FA practice increases the ability to identify thoughts (mind wandering) outside the field of focus (demands of a task) and redirect the focus. With continued practice of FA meditation one increases the awareness of internal mental states. One could argue that people who regularly meditate become experts at introspection. Therefore, FA meditation provides a valuable paradigm to investigate subjective experience to increase our knowledge of internal cognitive states such as mind wandering.

Open Monitoring Meditation

The second form of meditation is termed *open monitoring meditation*. An important element of OM practice is the initial practice of FA training to calm the mind and reduce distractions. FA advances the monitoring skill. When the monitoring skill is advanced, this skill becomes the main focus of transition into OM practice. The aim of OM practice is to remain only in the monitoring state. Which is the attentive state moment-by-moment to anything that occurs in experience (without focusing on an particular object). In order to reach this state the meditator gradually decreases the focus on an explicit object and a broader monitoring state is emphasized. There is an increased emphasis on cultivating a 'reflexive' awareness that allows greater access to the rich features of each experience (Lutz et al., 2008). An important distinction between FA and OM meditation is that in OM meditation the monitoring itself does not create any new *explicit focus*. Thus, OM involves no strong distinction between selection (focus on breath counting) and de-selection (mind wandering thoughts) as in FA meditation. OM meditation involves the effortless sustaining of awareness without explicit selection. It does not follow the cyclic process of mind wandering and shifting back to sustained focus on an object. For this reason, the relationship between OM and mind wandering is more complicated. The next chapters will focus on studies that investigated the effects of FA meditation on mind wandering and default network activity and connectivity.

3.3. Effects of mindfulness on cognition

There has been increased interest in the effects of meditation on cognitive abilities in scientific research. Chiesa and colleagues (2011) reviewed 23 studies on the effects of meditation on objective measures of cognitive functions (attention, memory, executive functions etc.). Overall, focused attention meditation was associated with significant improvements in selective and executive attention. Both practices have been found to improve working memory capacity (Mazak et al., 2013; van Vugt & Jha, 2011). Mindfulness meditation practice is also linked to improvement of cognitive flexibility (Moore & Malinowski, 2009). Mindfulness meditation has a positive effect on all attentional functions: sustained, selective and executive attention and attention switching. Furthermore, executive functioning is improved when practicing mindfulness meditation (Chiesa et al., 2011).

3.4. Is mindfulness the opposite of mind wandering?

Popular literature argued that mindfulness is the opposite of mind wandering. Mrazek, Smallwood & Schooler (2012) proposed that mindfulness and mind wandering appear to be opposing constructs with respect to the ability to maintain undistracted. There is consensus that sustained attention represent a fundamental element of mindfulness. In direct contrast to this, mind wandering is described as the interruption of focus on a current task. As described in chapter 2, mind wandering has many behavioural indicators that have a mindless quality. Such as rapid and automatic responding during performance tasks (Smallwood et al., 2004), absent minded forgetting (Smallwood et al., 2003) and eye movement during reading comprehension tasks that show little attention for the lexical properties of what is being red (Reichle et al., 2010). The ability to remain mindfully focused on a task therefore appears to be in direct opposition to the tendency for attention to wander to task-unrelated concerns. In words of Mrazek, Smallwood & Schooler (2012) '*where mindfulness ends, mind-wandering begins'*. However, the conceptual relationship between mindfulness and mind wandering seems more nuanced than this. A recent construct validation study of breath counting by Levinson and colleagues (2014) evaluated the discriminant validity of breath counting by assessing its correlation with mind wandering. The data suggest that mindfulness (indexed by breath counting) is not reducible to mind wandering's absence as is evident from the variance in breath counting accuracy unexplained by these measures of experience sampling. This data supports the view that mindfulness and task unrelated thoughts might coexist. However, thought probes (ES) used in this study to measure mind wandering might not be as valid as behavioural measures of mind wandering. All in all, popular literature underlines that mindfulness might be defined as the opposite of mind wandering. However, this idea needs great caution as no causal relationship between the presence of mindfulness and the absence of mind wandering is established. More research on the specific relationship between these two constructs is needed.

3.5. Conclusion

FA meditation provides a paradigm to investigate internal cognitive states such as mind wandering. Meditation practice has a highly introspective nature. The process of introspection that is involved in meditation basically involves observing one's own mind wandering. Since meditators acquire expertise in their mind wandering processes and thus might develop a different relationship with the content of it, meditation is an interesting topic for those who investigate the relationship of mind wandering and the default network. The next chapter will review the relationship between FA meditation and mind wandering.

Chapter 4. Effects of FA meditation on mind wandering

In this chapter the literature that describes the effect of FA meditation on mind wandering will be reviewed. Questions that will be discussed are: 1.Does FA meditation influences the temporal course of mind wandering? (i.e. reduce mind wandering episodes) 2. Does FA meditation influence the content of mind wandering?

4.1. Studies investigating the effects of FA meditation on mind wandering

Little is known about the effects of focused attention meditation on the process of mind wandering. The few studies that investigated the influence of meditation on mind wandering will be discussed in this paragraph. Mrazek, Smallwood and Schooler (2012) were the first to examine the impact of FA-meditation on mind wandering. They compared a group of participants that performed 8 minutes of FA meditation to two control groups: 8 minutes of passive reading and 8 minutes of relaxation. All groups then completed the same 10-minute Sustained Attention to Response Task (SART). The SART used in this study was a Go/No-go task in which participants were instructed to respond as quickly as possible to frequent non-targets (O's) by pressing a space bar and refrain from responding to (rare) targets (Q's). Two indirect measures of mind wandering were used in this study: SART errors (failures of omission to targets) and RT CV (Reaction Time Coefficient of Variability). According to a study of Chine et al. (2009) SART errors indicate more pronounced mind wandering than a large response time coefficient of variability. RT CV has been shown to reflect a state of mind wandering with minimally disruptive disengagement of attention (Cheyne et al., 2009). In this study, participants in the FA meditation condition showed significantly less SART errors and smaller RT CV than either comparison group (see figure 6). This data shows that FA meditation seems to diminish mind wandering during a current task. However, it is important to note that this is a mindfulness state effect that is measured. And based on these indirect measures of mind wandering it is not sure what subjects really are doing in the task.

What are the effects of more intensive and prolonged FA meditation training on mind wandering? Mrazek and colleagues (2013) examined whether a two-week FA meditation-training course would decrease mind wandering and improve cognitive performance on a GRE reading comprehension and working memory task compared to a control program (nutrition training) in students. Mindfulness training resulted in less probe- and self-caught mind wandering and retrospectively self-reported mind wandering during both tasks. Mindfulness training led to significant improvements in reading performance and working memory. Nutrition training did not cause changes in performance or mind wandering. The enhancement of performance was statistically mediated by reductions in mind wandering. In other words, the enhanced performance following FA meditation training results from a dampening of distracting thoughts in those who were prone to mind-wandering at pre-test.

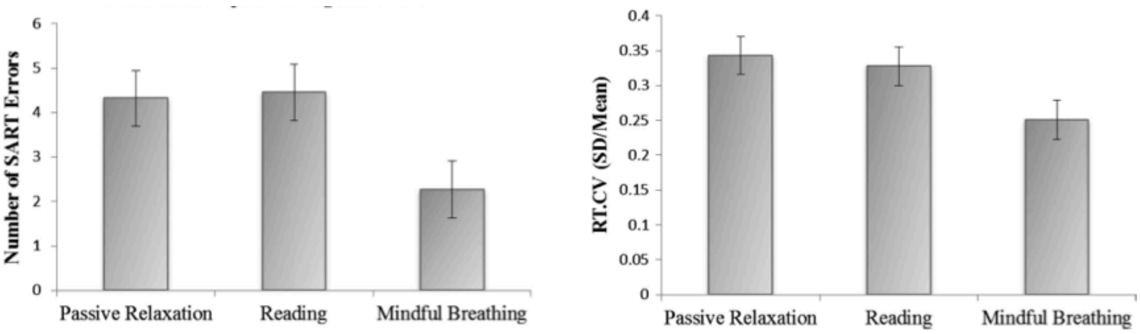


Fig 6. Reduction in mind wandering following mindful breathing (Mrazek, Smallwood & Schooler, 2012). Two behavioural measures during the SART indicated that 8 minutes of Mindfulness breathing reduced mind wandering compared to relaxation and passive reading. SART errors reflect errors of commission when a subject fails to withhold a response to rare non-targets. RT CV is calculated as the standard deviation of RT divided by the mean RT.

A study of Levinson and colleagues (2014) was the first to compare the effect of FA meditation on mind wandering between in experienced meditators and age-matched controls. Two experiments were conducted to investigate the relationship between breath counting (FA meditation) and mind wandering in long term meditators and age-matched controls. In the first experiment, 120 subjects had to focus on their breath and count breaths from 1 to 9 repeatedly during a meditation session of 25 minutes. With breaths 1-8 t subjects were instructed to press one button and on breath 9 to press another to measure counting accuracy. Counting accuracy was indexed as the percent of total task count sets correct. Every 90 seconds experience sampling probed state mind wandering on a 6-point likert-scale with the probe '*just now where was your attention?*' ranging from completely on-task to completely off- task. In this study, total task counting accuracy and state mind wandering (provided by the thought probes) were correlated across subjects. They observed that breath-counting accuracy was associated with less *self-reported* mind wandering across subjects. This relationship was examined at a finer timescale within subjects by investigating whether diminished mind wandering occurred during moments when mindfulness (indexed by accurate counting) was present. Average mind wandering ratings were compared from correct vs. miscount count probes within subjects and found that mind wandering decreased during moments of accurate counting.

In the second experiment changes in mind wandering were measured over the course of 20 consecutive days of either breath counting, n-back training (practice of working memory) or no training. The breath-counting group demonstrated decreased mind wandering and improved counting accuracy relative to the two control groups. The two control groups (n-back training and no training) did not differ from each other in pre-post measures of mind wandering. These findings suggest that FA meditation (measured by accurate breath counting) decreases mind wandering, especially during the moments when mindfulness is present (Levinson et al., 2014).

4.3. Conclusion

To date, there are few studies that investigated the effects of FA meditation on mind wandering. The studies that are known showed that a single session of FA meditation in meditation naïve participants seems to diminish mind wandering reflected by less errors and less reaction time variability on a Sustained Attention To Response Task (SART) (Mrazek, Smallwood & Schooler, 2012). Two weeks of FA meditation training resulted in less probe and self-caught mind wandering, increased reading comprehension and working memory performance in students (Mrazek et al., 2013); decreased mind wandering during moments of mindfulness (increased breath counting accuracy), both during a single session of FA meditation and after a course of 20 days of mindfulness training (Levinson et al., 2014). Thus, reasoning from these studies FA meditation seems to have an effect on mind wandering episodes by diminishing its occurrence. It is important to note that all of these studies investigated the effect of state mindfulness on mind wandering. None of these studies investigated the effects of FA meditation in experienced meditators and comparing it to meditation naïve controls. I propose that future research should focus on this.

There a no studies that investigated whether FA meditation influences the type of mind wandering and content of mind wandering thoughts. As discussed earlier in chapter 1, the content of mind wandering thoughts can be pointed down to two categories: *introspective/meta cognitive* based thoughts or *memory based construction/simulation* (Andrews-Hanna et al., O' Callaghan et al., 2015). Future research could investigate if FA meditation influences the occurrence of these two categories of mind wandering content. Furthermore, future studies could investigate if meditation might have an effect on ruminative thoughts of mind wandering, as there are studies that suggest that mindfulness meditation training has positive effects on depression and other psychiatric disorders, which are associated with rumination (Marchand, 2012; van Vugt et al., 2012). And higher levels of unhappiness are associated with mind wandering thoughts about the past (Poerio et al., 2013; Ruby et al., 2013a, Stawarczyk et al. 2013). It is important to note that only the studies of focused attention meditation were discussed here, open monitoring meditation (see chapter 3) might exhibit different effects on mind wandering.

Chapter 5. Mind wandering and the default network

As discussed in chapter 1, the default network is a set of brain regions that consistently shows higher activity at rest compared to tasks that require sustained attention for externally presented stimuli. In chapter 2 the psychological features of mind wandering were discussed. It remains a matter of debate to what precise cognitive processes the de default network corresponds to. A prevalent theory is that the recruitment of the default network is associated with internally focused thoughts, that occur in the form of mind wandering (Smallwood & Schooler, 2006). However, the neural basis of mind wandering remains currently debated (Mason et al.2007; Gilbert et al.2007; Andrews-Hanna et al., 2010). The aim of this chapter is to consider the role of the default network subsystems with respect to mind wandering. Four sub questions will be discussed to explore this relationship: 1). What is the empirical evidence for the role of the default network in mind wandering processes? 2). Do brain regions associated with mind wandering belong to a specific subsystem of the default network? 3). Is there convergence of brain regions between studies? 4). In what way does mind wandering relate to each subsystem? (I.e. what kind of mind wandering is associated with what subsystem?). I will explore the possibility that the distinct subsystems within the default network could be associated with different aspects of mind wandering.

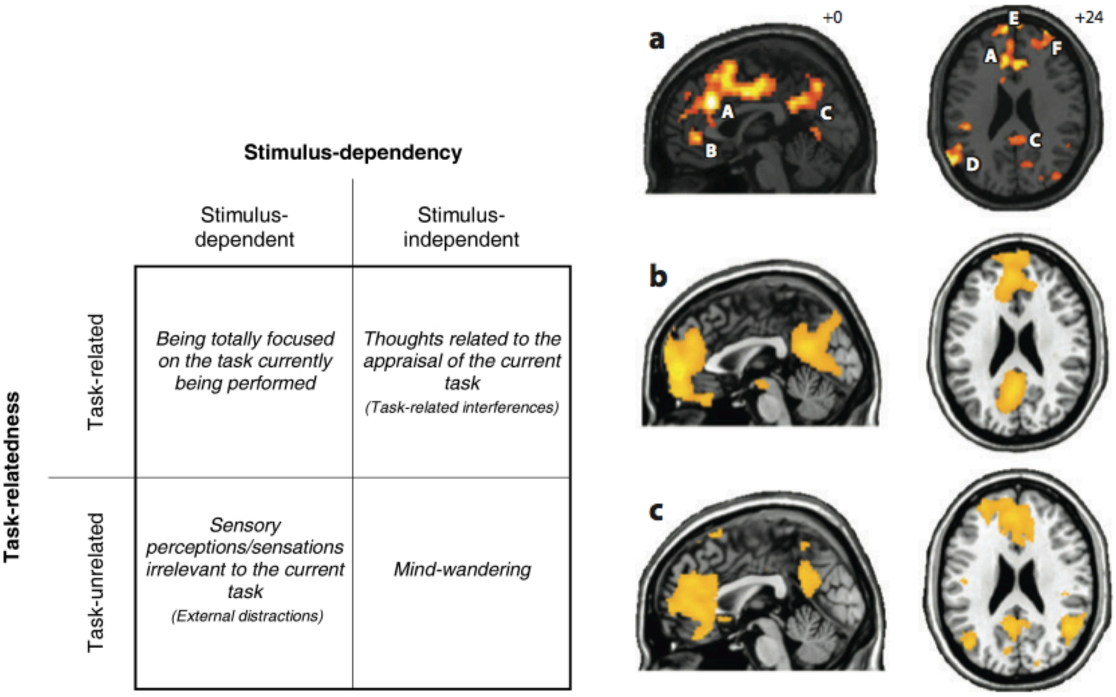
5.1. Studies on default network and mind wandering

The hypothesis that the default network plays a role in the generation of thought that occurs during mind wandering finds support from observations of fMRI studies. First (indirect) support for this hypothesis comes from studies where the default network shows a pattern of anti-correlation with the neural systems that are active during the performance of an external task (Fox et al. 2005; Fox & Raichle. 2007). Somewhat more direct support for the view that the default network is associated with mind wandering comes from neuroimaging studies showing correlations between the frequency of self-reported task-unrelated thought and default network activity (Mason et al. 2007). Mason and colleagues (2007) were the first to combine self-report on mind wandering (score on daydream frequency scale) with a (verbal & visuospatial) working memory task. They compared activity in the default network when participants performed practiced blocks to default network activity during novel blocks. The idea behind this design is that practiced blocks of the task are associated with high incidence of stimulus-independent thought (SIT); when the mind is most likely to wander. And novel blocks are associated with low incidence of SIT; when the mind is least likely to wander. The default network was functionally defined by comparing the baseline BOLD response (fixation) to the response of the task periods (novel and practiced working memory task). This comparison showed greater recruitment at rest of distributed network regions that included the PCC/precuneus, posterior lateral cortex, insular cortex, the cingulate, frontopolar areas and the dorsal medial and ventral medial PFC. These regions were therefore defined as areas of the default network. In order to investigate whether there is a relation between default network activity and mind wandering, this study measured how BOLD activity within this functionally defined network changed as a function of block type. They compared activity of practiced blocks to novel blocks. Default network activity was greater during high incidence SIT periods (practiced blocks). Regions of the DN that showed greater activity during high incidence SIT (practiced blocks) compared to low incidence SIT (novel blocks) were mPFC, PCC, precuneus. Not a single region showed greater activity during low-incidence SIT periods. The found activation in the *mPFC* and *PCC/precuneus* correspond to the core subsystem. Furthermore, stronger default network activity was found in subjects with a stronger tendency to mind wander during highly practiced task compared to new tasks.

Yet, this study inferred mind wandering only indirectly by collecting mind wandering self reports in a separate session outside the scanner (Mason et al., 2007). A big disadvantage of this is that there were no online measurement of mind wandering conducted. Therefore there is a possibility that the observed activity in the default network can be attributed to other factors than mind wandering. To overcome these limitations, Christoff and colleagues (2009) provided a direct empirical test to examine the hypothesis that the recruitment of the default network arises during the precise moment when the mind wanders away from the task at hand. In order to do so, they used the method of *online experience sampling* to fMRI research on mind wandering. To collect experience sampling reports of mind wandering during fMRI scanning, subjects were presented with thought probes while performing a simple go/no go task, known as a sustained attention to response task (SART). The task required the participants to respond to al non-target numbers (0-2 and 4-9) by pressing a button while suppressing their respond to a target number (3). Also, task performance errors were used as a measure of mind wandering. The analysis focused on the time interval preceding the experience sampling probes to dissociate the effects of mind wandering from the effects of answering a probe. The interval preceding a probe was categorized according to the subjects' response as either '*on task*' or '*off-task*'. Finally, the interval before each target was categorized according to a correct response (*correct withhold*) or incorrect response (*commission error*). Regions of the default network that were activated when episodes of mind wandering (intervals before off task probes) were compared with episodes of being on task (intervals on task probes) where the *PCC, precuneus, mPFC, TPC and TPJ (*figure 7a). Regions of the default network that were activated preceding SART errors (intervals before commission errors compared to correct withholds) were the *dorsal medial* and *ventral medial PFC*. These regions were both activated when participants were aware of their mind wandering (with meta awareness) and unaware (without meta-awareness) only to a lesser degree with meta-awareness. The TPJ, dmPFC and TPC are part of the dorsal medial subsystem (table 2).

Starwarczyk and colleagues (2011) elaborated on the study of Christoff and colleagues (2009). In the study of Christoff and colleagues (2009), participants were simply asked to report whether they were totally focused on the task (*on task reports*) or distracted by task unrelated thoughts (*off-task reports*). Stawarczyk and collegues (2011b) argued that this dual choice task fails to clearly distinguish between mind wandering, external distractions (i.e. sensory perceptions/sensations irrelevant to the current task) and task-related interferences (thoughts related to the appraisal of the current task). It might be that these three different types of conscious experience might have been mixed into the same response category in the study of Christoff et al (2009). In order to clarify the role of the default network in mind wandering (versus unfocused external attention and task related interferences) participants reported their experience in both *task-relatedness* and *stimulus-dependency* during the performance of the SART task. These two dimensions resulted in four possible classes of conscious experience (see figure 7 left panel). The brain regions that showed higher activity during mind wandering compared to task related interferences and external distinctions were *the medial prefrontal cortex, the PCC/precuneus and the left medial temporal gyrus* (see figure 7b). These regions correspond to the core subsystem. It is important to note that this study defines mind wandering as task unrelated thought. However, as discussed in chapter 2, there is evidence that the content of self-generated thoughts during mind wandering can also be task related. The brain area that is active in this study during task related inferences) is the ventral MPFC. The vmPFC is part of the medial temporal subsystem.

Allen et al. (2013) combined ES and an error awareness task (EAT) during fMRI. The EAT is a simple go/no go task of Hester et al. (2012). When aware of an error subjects pressed a button. Mind wandering was operationalized as task unrelated thoughts (TUTs). The regions that were active during increased reaction times (response inhibition) and increased TUTs were the *mPFC* and *the PCC*. These regions are part of the core subsystem of the default network. Furthermore, correct stop trials resulted in deactivations in the medial PFC and PCC, core subsystem of the default network (see figure 7c).



Task-relatedness		Stimulus-dependency	
		Stimulus-dependent	Stimulus-independent
	Task-related	*Being totally focused on the task currently being performed*	*Thoughts related to the appraisal of the current task* *(Task-related interferences)*
	Task-unrelated	*Sensory perceptions/sensations irrelevant to the current task* *(External distractions)*	*Mind-wandering*

Figure 7. Left Panel dimensions of on going experiences during externally driven task that require sustained attention according to 2 dimensions: task-relatedness and stimulus dependency (Stawarczyk et al., 2011). Right panel (a): (A= dorsal anterior cingulate cortex, B= ventral medial prefrontal cortex, C=posterior cingulate cortex, D= right temporal-parietal junction, E= dorsal medial prefrontal cortex, F= left rostral-lateral prefrontal cortex) (a) Christoff et al. 2009; (b) Stawarkzyck et al. (2011b) (c) Allen et al. 2013.

An exciting new study of O' Callaghan and colleagues (2015) is the first that explored both the frequency and phenomenological content of mind wandering episodes related to the subsystems of the default network anatomically defined by Andrews-Hanna et al (2012). They combined a new task, the shape expectation task, with resting state functional connectivity (MRI). The shape expectation task was designed to resemble conditions in everyday life that are most conductive to mind wandering. Subjects conducted no demanding task, but solely a thought sampling task to elicit more instances of mind wandering. In earlier studies only experimental assessment of mind wandering had taken place during performance on a concurrent task. Both the *frequency* and *qualitative content* of mind wandering were probed. Mind wandering content was categorized as either *introspection/metacognitive-based* or *memory-based construction/simulation*. This taxonomy was adapted from the studies of Andrews-Hanna and colleagues (2012) and points towards the functional anatomical specialisation of the subsystems, where the *dorsal medial prefrontal subsystem* is linked to a *introspective/metacognitive*-based style of mind wandering and *the medial temporal* lobe subsystem is associated with memory based construction/simulation mind wandering. Overall, in 37% of the trials occurrences of mind wandering were reported. Furthermore, figure 8 displays the proportion of memory-based construction/simulation versus introspective/metacognitive-based content. These results show that mind-wandering trials contained (convincingly) more instances of memory-based construction/simulation (68%) than introspective-based content of mind wandering (32%). The authors suggest that this is in keeping with reports of thoughts orienting the future. The tendency to mind wander in a *memory-based constructive/simulation* manner was associated with increased connectivity between the *TempP* and the *HF*. These regions are part of the *dorsal medial* (TempP) and *medial temporal subsystem* (HF). They did not find a significant relationship between introspective/metacognitive based mind wandering and specific regions of the dorsal medial subsystem. Instead, the tendency to mind wander in an *introspective/ metacognitive* manner was associated with increased connectivity between the medial temporal (HF) and core (PCC). Additionally, the results revealed that stronger *dorsal medial connectivity* (LTC & TempP) coupled with relatively weaker connectivity of medial temporal (PHG) regions to the core subsystem (PCC) was associated with *mind wandering frequency*. This study represents the first attempt to asses mind wandering (both frequency and content) to the distinct patterns of the subsystems in the default network of the brain. Unfortunately, the two categories of mind wandering content (introspective-metacognitive based/memory based simulation) did not correlate with activity patterns in the distinct subsystems (dorsal medial subsystem and medial temporal subsystem).

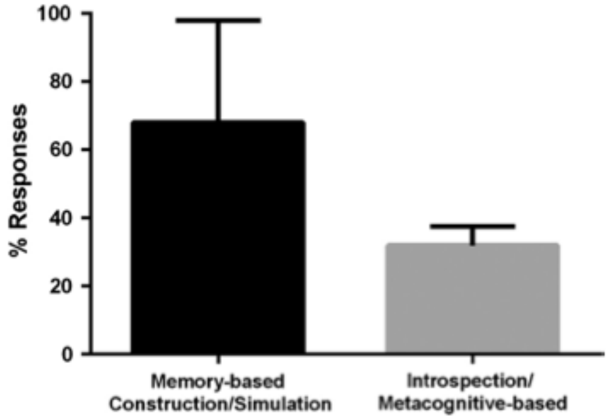


Fig 8. Proportion memory-based construction/stimulation content of mind wandering vs. introspective / metacognitive based content. Means and standard error (n=31) O' Callaghan et al. (2015).

Table 3. Overview of the studies that investigated the association between mind wandering and the default network

Reference	**Technique**	**Task**	Active Brain Areas	**Subsystem**
Mason et al. (2007)	fMRI	Score on daydream frequency scale + practiced working memory task (high incidence of MW	*mPFC, , PCC,* precuneus,	Core
Christoff et al. (2009)	fMRI	- ‘ off task’ MW reports	PCC, precuneus, *TPJ, TPC, mPFC*	Core & DM
		- SART errors	dmPFC, vmPFC	DM & MT
Stawarczyk et al. (2011)	fMRI	Task unrelated MW	mPFC, PCC, precuneus, left medial temporal gyrys	Core
		Task related MW	vmPFC	MT
Allen et al. (2013)	fMRI	Increased TUT’s * & increased RT	mPFC, *PCC,* superior parietal lobe /	Core
O’ Callaghan et al. (2015)	RS-connectivity fMRI	**MW Frequency**	↑ LTC, TempP	↑DM
		MW Content Memory based construction/simulation	↑TempP & HF	↑DM & MT
		Introspection/ meta-cognitive based	↑HF & PCC	↑MT & Core

* Brain regions in *italic* are the regions corresponding to the subsystem (of Andrews-Hanna et al., 2014), Core system = green, Dorsal Medial (MT) = red, Medial Temporal (MT) = blue. ↑ increased connectivity, ↓ decreased connectivity. mPFC= medial prefrontal cortex, ACC= anterior cingulate cortex, PCC= posterior parietal cortex, TPJ = tempoparietal junction, dmPFC = dorsolateral prefrontal cortex, TPC= tempoparietal cotex, LTC= lateral temporal cortex, TempP= temporal pole, PHG = parahippocampal gyrus, HF = hippocampal formation. TUT= task unrelated thoughts, MW= mind wandering.

5.2. Conclusion

This chapter aimed to explore the possibility that the distinct subsystems within the default network could be associated with different aspects of mind wandering.

The *medial temporal subsystem* consists of the *HF+, PHC, Rsp, IPL and vmPFC* (see figure 9). Based on the reviewed studies in this chapter, table 4 shows that this subsystem is related to task unrelated mind wandering (Stawarczyk et al., 2011). More specifically, this subsystem is associated with memory related construction of mental imagery (O' Callaghan et al., 2015). However, the existing evidence does not synthesize a clear outcome to what specific component of mind wandering the medial temporal subsystem is related.

The *dorsal medial subsystem* of the default network consists of the *TempP, LTC, TPJ* and *dmPFC* (see figure 10). Table 4 shows that this subsystem is associated with probes reporting 'off task' (versus on task) mind wandering and errors on a Sustained Attention To Response Task (Christoff et al., 2009) in one study. Increased connectivity of regions of the dorsal medial subsystem is associated with mind wandering frequency (O' Callaghan et al., 2015). However, the existing evidence reviewed in this chapter does not come forward with a specific component of mind wandering that is processed by the dorsal medial subsystem.

All studies revealed the implication of the *core subsystem* in mind wandering processes (see table 4). The core is activated in all studies that measure mind wandering when participants performed a concurrent attention-demanding task. I suggest that this reflects the implication of the core system in shifting between internal (mind wandering) and external information. An unexpected finding is the fact that increased connectivity between the core and medial temporal subsystem is associated with introspective/meta cognitive based thoughts (O' Callaghan et al., 2015). This is not in line with earlier studies suggesting that the dorsal medial subsystem plays an important role in introspective based thoughts (Andrews-Hanna et al., 2014). However, this is the first study attempting to develop a task, designed specifically to explore the relationship between two dissociable styles of of mind wandering content and its distinct subsystems. This study awaits replication in a larger cohort. Based on the reviewed studies, the core system cannot be attributed to a specific mind-wandering component.

Mind wandering is a complex phenomenon to investigate in an experimental setting, due to its spontaneous and internally directed nature. Most studies discussed in this chapter explored the general qualitative forms of mind wandering and default network activity. Turning our attention to the *quantitative* aspects of mind wandering content, an interesting finding in the study of O' Callaghan and colleagues (2015) is that participants engaged in *memory based/ constructive* modes of thought most of the time, opposed to *introspective/metacognitive* styles of mind wandering. This type of mind wandering is thought to be implicated in memory-related processing ('*This reminds me of the vacation we spend in France'*), mental imagery and scene construction ('*I wonder what I am going to eat later on'*). It is correlated to the medial temporal subsystem. In the study of O' Callaghan et al. (2015) the tendency to mind wander in a constructive/simulation based manner reflected increased connectivity within the MTL subsystem. This finding is in accordance with the functional correlational analysis of Andrews-Hanna et al. (2010) (see chapter 1).

Table 4. Relationship between subsystem and mind wandering

Medial Temporal	**Dorsal Medial**	**Core**
Task unrelated MW	'Off task' MW reports	SIT's during practiced WM task
Introspection/ meta cognitive *correlation with core*	SART Errors	'Off task' MW reports
Memory Based content	MW Frequency	Task unrelated MW
	Memory based construction *correlation with MT*	Increased TUT's
		Increased RT during error awareness task
		Introspection/meta cognitive *correlation with MT*

SIT= Stimulus independent thought, MW= mind wandering, MT= medial temporal subsystem, DM= dorsal medial subsystem. WM= working memory.

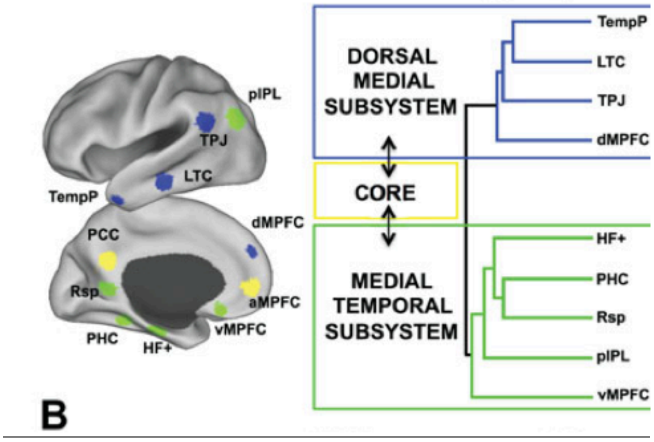


Fig 9. The distinct subsystems of the default network adapted from Andrews-Hanna et al (2014).

Chapter 6. Effects of Focused Attention Meditation on the default network

The neural mechanisms underlying FA meditation have not been well characterized. A review of Marchand (2014) on the literature on the neural mechanisms of meditation revealed evidence that meditation impacts the function of the *medial (prefrontal) cortex* and associated default network (Marchand, 2014). Furthermore, meditation practice seems to have an effect on lateral frontal regions, the *posterior parietal cortex/precuneus (PCC)* and the *inferior parietal lobe (IPL)*, at least in several studies (Marchand, 2014). Although many questions remain unanswered, the current literature thus provides some evidence that FA meditation modulates regions of the default network. The aim of this chapter is to increase our understanding of the relationship between FA meditation and the distinct subsystems of the default network. I will review the recent literature on FA meditation by relating it to the three subsystems. The questions that will be discussed in light of the literature are: 1. Does meditation has an effect on the temporal nature of the phases described in the meditation-model of Hasenkamp et al. (2012) (chapter 3) and especially on default network activity during the mind-wandering phase? 2. Does meditation modulate the corresponding activation of brain areas of the default network implicated in mind wandering? 3. Can these effects be translated to the different subtypes of the default network?

6.1. The cognitive cycles of meditation and its corresponding neural correlates

Hasenkamp and colleagues (2012) presented a basic theoretical model of cognitive fluctuations between mind wandering and attentional states derived from FA meditation practice (see figure 10). This model contains four dynamic cognitive states of a cognitive cycle: 1. Mind wandering state 2. Awareness of mind wandering, 3. Shifting of attention and 4. Sustained attention. To investigate the neural correlates of the four cognitive states, Hasenkamp and colleagues (2012) instructed meditation practitioners to perform breath focused meditation in the fMRI scanner. When the participants realized their mind had wandered, they pressed a button and returned their focus to their breath. Analyses showed activity in regions of the default network (*the posterior parietal cortex (PCC), medial PFC, posterior parietal/temporal cortex and parahippocampal gyrus*) were enhanced during the *mind wandering* phase (MW). These regions are part of the core subsystem (mPFC/PCC) and the medial temporal subsystem (PHG). The aware phase revealed activations in the anterior and posterior insula and the dorsal ACC (in addition to the expected motor-related activations). According to Hasenkamp et al. (2012) these regions are consistent with the *salience network*, a subdivision of the attention network (involved in detecting relevant or salient events). Thus, the activity found in the ACC and insula during mind wandering might reflect the awareness that the mind has wandered (meta-awareness). During the *shift phase*, when participants redirect their attention from mind wandering back to the breath, activity was shown in the *dorsa*l and *ventral PFC* and *lateral inferior parietal cortex (IPC)*. These regions are consistent with the executive network (the network that acts on relevant stimuli detected by the salience network). During maintenance of attention in the *focus phase* the *dorsolateral prefrontal region* of the executive network remained active. Interestingly, activations during the four cognitive phases were modulated by lifetime experience. There was significantly lower activity in participants with more practice experience. Activity in the shift phase was significantly correlated with practice time, suggesting that reorienting of attention is a primary cognitive skill that FA meditation trains. However, it is important to note that the regions associated with the SHIFT phase (*ventral lateral PFC and lateral inferior parietal cortex (IPL)*) in the study of Hasenkamp et al. (2012) are part of the *medial temporal subsystem* of the default network according to the consistently shown data described in Andrews-Hanna et al. (2014) (see Chapter 1, table 1).

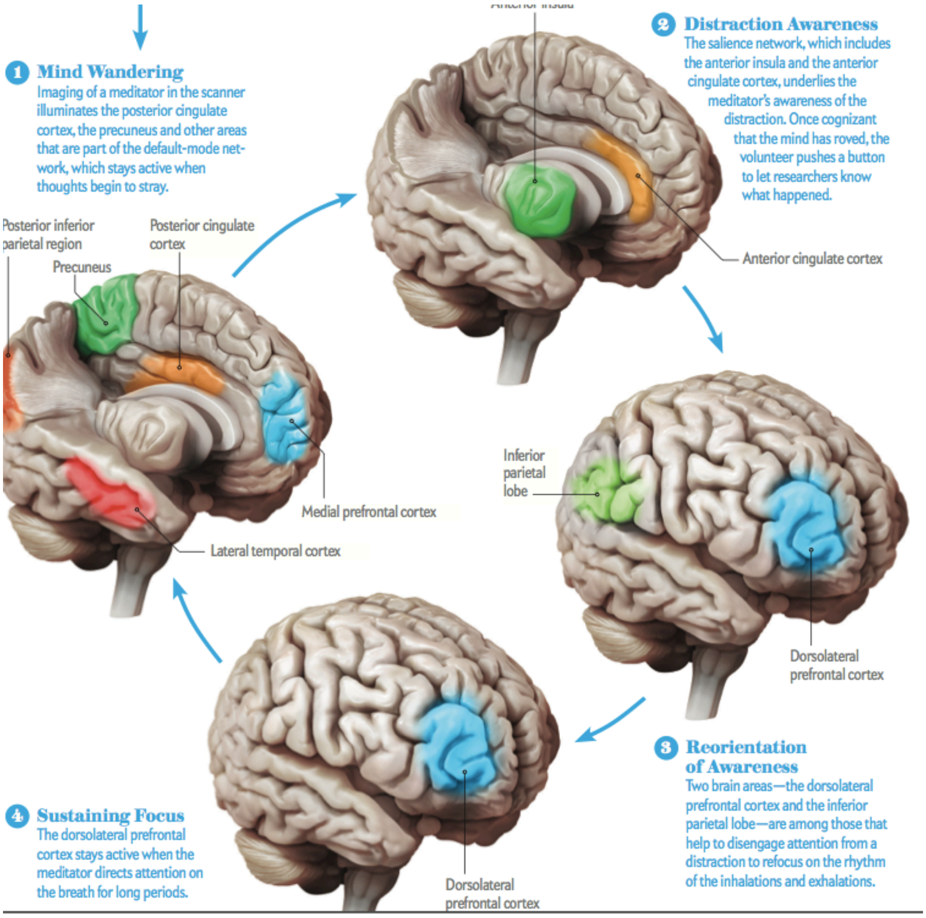


Figure 10. Cycle of events during FA meditation and the corresponding activation of specific brain areas (from Ricardo, Lutz & Davidson, 2014).

6.2. Does FA meditation alter the response duration in default network subsystems?

Pagnoni, Cekic & Giu (2008) investigated the duration of neural activation of different brain regions during FA meditation in practitioners and matched control subjects. They used fMRI and a simplified meditative condition (focus on breathing throughout and return to it when distracted from it) interspersed with a lexical decision task; the meditative condition was interrupted at random periods by a string of letters. Subjects had to indicate if it was a real English word or not. Zen practitioners showed a decreased duration of the BOLD response in regions of the default network compared to the control group. These regions included the *posterior cingulate cortex, anterior cingulate cortex (Cortical midline structures).* These regions can be attributed to the core subsystem of the default network. A possible explanation for this finding is that meditators had an advantage over control subjects in the meditative task of re-focusing attention on the breath after having processed and responded to the presented stimuli. It is interesting to note that the BOLD signal drops to a level *below* baseline in the post stimulus period in the PCC in meditators and not controls. However, behavioural performance on the lexical decision task did not differ between groups. There were no differences in reaction times or errors between meditators versus controls. Thus, FA meditation might decrease the duration of default network activity, especially the core subsystem. See table 5 for an overview of all studies and their findings.

6.3. Does meditation alters activity in the distinct default network subsystems?

Taylor and colleagues (2011) investigated the effects of FA meditation on the neural responses to emotionally stimuli in experienced and beginner meditators. In experienced meditators, meditation induced a deactivation of default mode network areas (*medial prefrontal and posterior cingulate cortex*) across all valence categories (negative, positive, neutral pictures) and did not influence responses in brain regions involved in emotional reactivity during emotional processing. This deactivation corresponds to a deactivation in the core subsystem of the default network (see table 5).

A study of Brewer and colleagues (2011) investigated brain activity in experienced meditators and matched meditation-naïve controls as they performed FA meditation. They found that the main nodes of the default network (*mPFC and PCC*) were deactivated in experienced meditators and not in meditation naïve controls during meditation. As noted above, these nodes are associated with the core subsystem. However, it remained unclear whether focused attention meditation practice influences functional connectivity. Therefore, Brewer et al. (2011) also conducted a functional connectivity analysis in their study (Brewer et al., 2011). The analysis revealed stronger coupling in experienced meditators between the PCC and dmPFC, both at baseline and during meditation. These regions correspond to the core subsystem. Furthermore, experienced meditators reported less mind wandering during meditation compared to controls. Consistent results were shown across resting-state baseline and meditation conditions (see table 5).

Another connectivity study of Taylor and colleagues (2012) showed that experienced meditators relative to beginners showed *weaker* functional connectivity between the a) *mPFC & left Inferior Parietal Lobe/Ventral mPFC (medial temporal subsystem)*, b) *left Inferior Parietal Lobe & PCC (medial temporal subsystem and core)* and c) *vmPFC & Inferior Temporal Cortex*. These areas are part of the *medial temporal subsystem*. This finding supports the idea that FA meditation decreases activity and connectivity of the medial temporal subsystem.

6.4. Does FA meditation improves control over default network activity?

A study of Garrison et al. (2013) tested a new method to link objective and subjective data by using real time fMRI (rt-fMRI). They provided participants with real-time feedback of Posterior Cingulate Cortex (PCC) during a focused attention meditation task. Experienced meditators and non-meditators were provided real-time feedback from the PCC or a control region during a focused attention meditation task (focus on the breath). Meditators were able to volitionally decrease the feedback graph, as assessed by deactivation of the posterior parietal cortex (PCC). In other words, meditators showed significant PCC deactivation when asked to volitionally decrease the feedback graph. In contrast, non-meditators did not show PCC deactivation when asked to volitionally decrease the feedback graph.

Another study of Garrison et al. (2013) used real time fMRI Neurofeedback and experience sampling to assess how the first-person experience of meditation relates to neural activity in the PCC. They found that PCC *deactivation* was associated with the factors of '*undistracted awareness'* and '*effortless doing'*, and that PCC *activation* was associated with *distracted awareness* and *'controlling'*. These factors were derived from self-report transcripts of the meditators during the meditation phase and feedback graphs. These findings support the hypothesis that meditation improves control over the default network, more specifically the core subsystem. See table 5 for an overview of the studies on the next page.

Table 5. Overview of functional imaging studies of focused attention meditation

Ref.	**Year**	**Technique**	**Meditation Sample**	**Average total practice hours**	**Results** **During focus**	**Results** **During distraction**	**Sub-system of DN**
Pagnoni et al.	2008	fMRI	12 experienced meditators vs 12 controls	> 3 years of practice	/	↓ MCC, PCC	↓Core
Taylor et al.	2011	fMRI	12 experienced meditators	1709 ± 694 **	↓mPFC & PCC	/	↓Core
Brewer et al	2011		12experienced vs. 13 meditation naive controls	10,565 ± 5,148	↓mPFC & PCC ↑ PCC & dmPFC	/	↓Core ↑Core & DM
Hasenkamp et al.	2012	fMRI	14 experienced meditators	>1 year regular practice	**Focus:** ↑dl PFC **Shift:** ↑dl PFC, IPL **Aware** ↑insula & ACC	**M-W** (unaware) ↑PCC, mPFC, PCC/TC, PHG	↑Core & MT (during MW)
Taylor et al.	2012	Functional connectivity	13 experienced meditators	6519 ± 14 445 **	↓IPL/V MPFC & IPL ↓dmPFC & vMPFC		↓MT ↓DM & MT
Garrison et al.	2013a	Real time fMRI	22 meditators vs. 22 non-meditators	9249 ± 1449 *	↓PCC		↓Core
Garrison et al.	2013b	Real time fMRI	10 experienced meditators	10.567 ± 4276*	↓PCC	↑PCC	↑Core

* Total average practice hours, Mean ± standard error of the mean , ** standard deviation , Core system = green, Dorsal Medial (MT) = red, Medial Temporal (MT) = blue ↑ increased connectivity, ↓ decreased connectivity, ↑activation, ↓ deactivation , ↓decreased duration response

6.5. Conclusion

Core subsystem

The reviewed studies reveal compelling evidence that FA meditation impacts the activity of the core subsystem of the default network. Studies of Taylor et al (2011) and Brewer et al. (2011) show decreased activation in experienced meditators of the core system. Pagnoni et al. (2008) found a decreased duration of the BOLD response of regions of the core subsystem. Taylor et al. (2011) found a deactivation of the core subsystem (the mPFC & PCC) in experienced meditators. Brewer and colleagues (2011) replicated the deactivation of the core regions of the default network. Furthermore they found increased connectivity within the regions of the core subsystem. Garrison and colleagues were the first to link real time fMRI neurofeedback to the subjective experience of experienced meditators. They found that meditators showed significant PCC deactivation when asked to volitionally decrease the feedback graph that was presented to them. In contrast, non-meditators did not show PCC deactivation when asked to volitionally decrease the feedback graph. This deactivation of the PCC is linked to the subjective experience of *undistracted awareness* of the meditator. Activation of the PCC is linked to the subjective experience of *distracted awareness*. Thus in light of this study one could argue that meditators might gain control over the activation of the cognitive processes corresponding to core regions of the default network (see chapter 7). Suggesting that experienced meditators might switch more voluntary between internal and external information (thus between sustained attention to an external stimuli or internal experiences). All in all, these findings suggest that activity in core system of the default network seems to be dampened and less frequently activated by FA meditation in experienced meditators. An important limitation of the existing studies is that no distinction made between the regions of the medial Prefrontal Cortex (mPFC), such that we could not distinguish dorsal medial PFC from ventral medial and anterior medial PFC. The dmPFC is part of the dorsal medial subsystem, the ventro medial PFC is part of the medial temporal subsystem and the anterior medial PFC corresponds to the core subsystem according to the functional anatomic fractionation of the default network (Andrews-Hanna et al., 2012). Thus the areas of the mPFC that are suggested to correspond to the subsystems must be interpreted with caution.

Medial temporal subsystem

To my knowledge, there is only one single study that investigated the effect of FA meditation on regions of the medial temporal subsystem of the default network. This functional connectivity study included seed regions of the medial temporal subsystem in the analysis.

The results show that decreased connectivity is found within the medial temporal subsystem (Taylor et al., 2012). Furthermore, decreased connectivity is found between the medial temporal and dorsal medial subsystem (Taylor et al., 2012). This might indicate that FA meditation might decrease memory based construction/ simulation by decreasing connectivity of the medial temporal subsystem. This interpretation is highly speculative. Future research should include regions of the medial temporal subsystem into their analysis in order to investigate what effects FA meditation has on this subsystem.

Dorsal medial

There are two studies reviewed that reported effects of the dorsal medial subsystem. Brewer and colleagues (2011) reported increased connectivity between regions of the dorsal medial and the core subsystem. Taylor and colleagues (2012) reported decreased connectivity between the dorsal medial subsystem and medial temporal subsystem. The increased coupling between regions of the dorsal medial and the core subsystem coupled with the decrease in connectivity between dorsal medial and medial temporal subsystem might be related to a predominance of introspective/meta cognitive mind wandering thoughts in meditators.

All in all, it is important to investigate the effects of meditation on the different subsystems as up till now the studies have not yet taken into account the different subsystems of the default network but rather elaborated on the old idea of the default network as a homogenous network existing of the mPFC and PCC. The connectivity study of Taylor et al. (2012) and Brewer et al. (2011) are promising first studies that explored more regions of the default network that can be attributed to subsystems of the default network. Future studies investigating the relationship between FA meditation and the default network should elaborate on the new idea of the default network as a heterogeneous network with three distinct subsystems.

Chapter 7. Default network, mind wandering and meditation: an integration

De default network consist of different subsystems that are active during passive moments of rest opposed to during performance of externally-oriented tasks The aim of this review is to clarify the function of the default network subsystems by relating it to mind wandering and meditation. Based on the reviewed literature, what do we know about the individual role of these three distinct subsystems in relation to mind wandering? And how do the distinct default network systems relate to meditation?

7.1. Dorsal medial subsystem

The dorsal medial subsystem consists of the dorsal medial prefrontal cortex, tempo-parietal junction, lateral temporal cortex and the temporal pole. It plays an important role in introspective/meta-cognitive based thoughts about the self and the other (Andrews-Hanna et al., 2014). The reviewed studies show that activity of the default network is related to mind wandering. How is the dorsal medial system then related to specific mind wandering aspects? The assessment of the phenomenological content of mind wandering has been mostly limited to broad categorisation methods, such as temporal orientation of mind wandering thought and degree of stimulus/task relatedness of thought, and limited attempts to map potentially dissociable forms of internally focused thoughts (mind wandering) onto the established default network subsystems. The specific functional role of the dorsal medial subsystem cannot be synthesized by the reviewed literature as these studies mainly used indirect measures of mind wandering or investigated qualitative aspects of mind wandering. However, there are indications that the dorsal medial subsystem is implicated in mind wandering thoughts in an introspective/ metacognitive way. Introspective/metacognitive mind wandering is broadly described as introspection about the mental states of self or others. Thoughts such as "*I feel good*" or " *She looks anxious, I wonder what is going on*'. A second aim of this review is to review the role of the dorsal medial subsystem in relation to FA meditation. The effect of FA meditation on mind wandering has found a general decrease of mind wandering episodes. This decrease in mind wandering has not been related to a specific subsystem of the default network in existing literature. Based on the idea that meditation is a method for introspection and that the dorsal medial subsystem plays a role in introspective thoughts, I suggest that FA meditation causes a predominance of *introspective/metacognitive* mind wandering thoughts reflected by an increase of dorsal medial subsystem activity.

7.2. Medial temporal subsystem

The medial temporal subsystem includes the hippocampal formation, the parahippocampal gyrus, the retrosplenial cortex, the posterior inferior parietal lobule, and the ventromedial prefrontal cortex. The medial temporal lobe subsystem facilitates construction of imagined scenes based on memory. For the same reasons as discussed for the dorsal medial subsystem, the specific functional role of the medial temporal subsystem is not clear based on the reviewed literature. However, the reviewed literature provided some evidence that memory-based construction mind wandering is mediated by the medial temporal subsystem. This mode of mind wandering has been associated with mental imagery; scene construction and memory related processing. For example, when imaging oneself in future situations, planning upcoming activities or remembering a past experience. There are indications that individuals engage more in memory based/constructive modes of thought during mind wandering, opposed to introspective/meta cognitive styles. Thus a predominant style of mind wandering in healthy adults seems to be in a memory-based construction manner. This style of mind wandering is associated with temporal lobe functional connectivity. The effects of FA meditation on this specific style of mind wandering have not been investigated (yet). However, weaker connectivity in the medial temporal lobe system is found in experienced meditators in two studies.

7.3. Core subsystem

The core system includes the posterior cingulate cortex and the anterior medial prefrontal cortex. The core subsystem is assumed to be an important zone of integration between the dorsal medial and medial temporal subsystem. It is thought to asses personal significance of incoming information, allowing an individual to integrate their current mental state with prior conceptual and episodic knowledge into an overarching personal meaning. Furthermore, it plays a role in shifting attention between salient internal input (thoughts, sensations etc.) and salient information in the external world. In other words, it is implicated in shifting between mind wandering and attention to external stimuli. The core is activated in all studies that measure mind wandering when participants performed a concurrent attention-demanding task. I suggest that this reflects the implication of the core system in shifting between internal (mind wandering) and external information. Most studies investigating the effects of FA meditation on default network activity revealed that FA meditation practice induced dampening of the core subsystem. If the core system is associated with switching between mind wandering and attention in meditation, the deactivation of the core might indicate less switching between internal and external information, and thus reflect less mind wandering The reduced response duration of the core system in experienced meditators might be interpreted as that they might reflect briefer mind wandering periods.

7.4. Future research agenda

The neuroscientific study of meditation is clearly still in its infanthood. The initial findings reviewed earlier promise to reveal the mechanisms by which it exerts its effects on mind wandering and to underpin the brain circuits that underlie this complex mental function. In my view, an important direction of future research is to investigate the relation of these subsystems with the two broad categories of mind wandering content (introspection/meta cognitive based vs. memory based construction) during meditation in experienced meditators and healthy controls. To address this gap in the literature, I suggest to elaborate on the study of O' Callaghan and colleagues (2015) and combine a thought sampling task with resting state functional connectivity. This task is designed to resemble the conditions that are most conductive to mind wandering. Namely, minimal external stimulation and free from constraints of performing a concurrent cognitive task. The subjects' only instruction will be to look at the screen and relax for 60 seconds, before the directed probe will appear on the screen. Subjects are then asked to report their thoughts on the previous trial. Participants may report any thought they have. Spontaneous thoughts will be classified according to the predominant content type on two dimensions, either introspection/metacognitive based thoughts or memory based construction/simulation. Each subject's proportion of introspective/meta cognitive based content versus memory-based construction/simulation will be determined with respect to their total instances of mind wandering. The relationship between default network connectivity and mind wandering content in both experienced meditators vs. controls will be explored. I expect a higher proportion of *introspection/meta cognitive based* thoughts in experienced meditators will be found, which will be reflected by stronger connectivity of the *dorsal medial subsystem*. As in the study of O' Callaghan et al. (2015) I expect a higher proportion of memory-based construction/simulation in controls reflected by increased connectivity of the medial temporal subsystem. Figure 11 and 12 display the expected results of memory-based construction vs. introspective/metacognitive-based content in experienced meditators vs. controls. It is important to note that I have no specific expectations about the absolute proportion of content in both groups. I solely expect a relative difference between the two types of content between both groups (i.e. interaction effect).

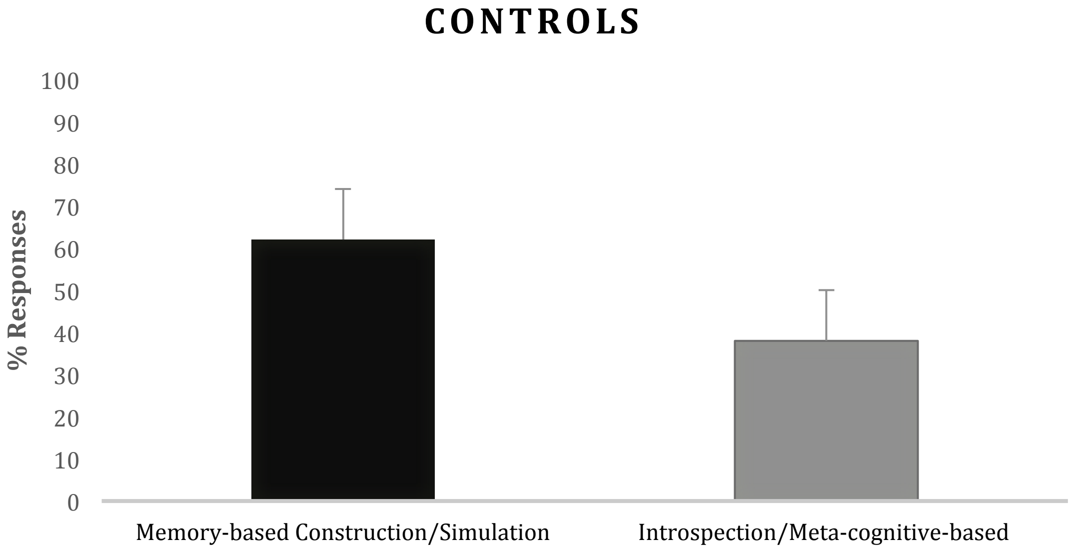


Fig. 11. Expected proportion of memory-based construction/simulation content versus introspective/metacognitive based content in controls. Means (standard error)

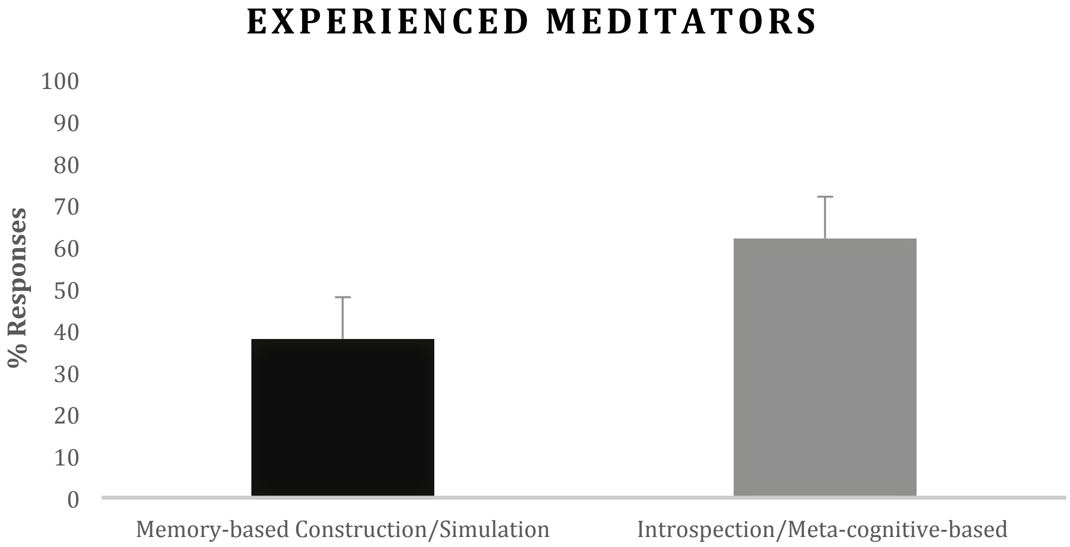


Fig 12. . Expected proportion of memory-based construction/simulation content versus introspective/metacognitive based content in experienced meditators. Means (standard error)

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