

IS THE SENSE OF SELF A THREAT TO WELL-BEING?

The Default Mode Network and Self-related Processing in Depression and Meditation

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Abstract

This literature review examines the default mode network (DMN) and how its role in self related processing and narrative selfhood relates to well-being. The essay explores the DMN in three levels of activity: Firstly in normal function, where mind-wandering is positively correlated with dissatisfaction; Secondly its abnormal function in depression, characterized by excessive activity and rumination; Thirdly in its arguably improved function during mindfulness and meditation, where lower activity is associated with higher well-being, decreased mind-wandering and altered sense of self. The essay shows a relationship between the DMN and well-being, where higher activity correlates with lower well-being.

Keywords: Default mode network, DMN, well-being, mind-wandering, the narrative self, mindfulness, meditation, depression

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Glossary

ACC	Anterior Cingulate Cortex
Anterior Insula	Important for interoception and switching attention between the DMN and CEN. Part of the SN.
CEN	Central Executive Network. A brain network that engages during focused attention.
dlPFC	Dorsolateral Prefrontal Cortex. Important for focused attention and cognitive control. Part of the CEN.
DMN	Default Mode Network
dmPFC	Dorsomedial Prefrontal Cortex. Part of the DMN and important in theory of mind.
Dorsal ACC	Important for redirecting attention between DMN and CEN.
IPL	Inferior Parietal Lobule. A core hub of the DMN.
1PFC	Lateral Prefrontal Cortex. Part of the CEN.
LTC	Lateral Temporal Cortex. Part of the DMN. Active during semantic and conceptual reasoning.
mPFC	Medial Prefrontal Cortex. A core hub of the DMN.
MTL	Medial Temporal Lobe. Part of the DMN and important for autobiographical memory.
PCC	Posterior Cingulate Cortex. A core hub of the DMN.
SN	Salience Network. Allocates attention between the DMN and CEN. Part of the task positive network.
Subgenual ACC	Active during negative emotion. Becomes part of the DMN during depression.
Task Positive Network	Network that is activated during external attention. Consists of the CEN and SN.
ТРЈ	Temporal- Parietal Junction. Integrates sensory and conceptual information.
vmPFC	Ventromedial Prefrontal Cortex. Important for emotion and evaluation.

Is the Sense of Self a Threat to Well-Being

The idea that "being present" makes us feel good is both a modern cliché and ancient wisdom. For millennia eastern religious and contemplative traditions, Buddhism in particular, have systematically explored and practiced this capacity, and developed a range of techniques that are today known as meditation (Kabat-Zinn, 2003). However, Buddhist traditions do not meditate just to feel good. They do it with the explicit goal of dissolving the sense of self (Millière, Carhart-Harris, Roseman, Trautwein, & Berkovich-Ohana, 2018). From a western perspective this raises a couple of questions: First of all, how and why is being present in the present related to well-being? And furthermore, what is the relationship between being present and the sense of self?

Though there have been various conceptualizations of the self this paper will distinguish between two different aspects of the self that are grounded in neuroscience: experiential self-reference and narrative self-reference. Experiential self-reference is when one is being present in the immediate perceptual and somatosensory experience. On the other hand, narrative self-reference corresponds to thinking and mind-wandering, which generally consists of inner narration or mental imagery. These thoughts form a narrative which links experiences together across time and space, thereby forming a sense of self that extends from the past into the future (Farb et al., 2007; Lieberman, 2007). These two modes of the self are not equal in their effect on well-being, rather the opposite. The narrative self is expected to diminish well-being and is the "threat" alluded to in the title. Experiential self-reference on the other hand, is expected to increase well-being and is equivalent to "being present". The two selves are also opposite in their moment to moment implementation in the brain since only one of them can be active at a time: either one is present in the here and now or one is lost in thought (Fox et al., 2005;

Vanhaudenhuyse et al., 2011). Using this terminology of the self it is possible to look at the Buddhist ideas of self and well-being in the light of science. What Buddhists appear to pursue through meditation is to inhibit thinking by a complete focus on their immediate experience. In other words, narrative self-reference is blocked out by activity of experiential self-reference to such a degree that the narrative aspects of selfhood dissolve.

The reason why narrative self-reference is hypothesised to decrease well-being is based on three observations which all point to the direction of "living in the moment" being conducive to happiness. The first is the scientific investigation of meditation which has linked the practice to increased well-being (Brown & Ryan, 2003) both during active meditation and at baseline in experienced meditators (Brewer et al., 2011). Meditation trains being present in the present moment, decreases mind-wandering, and by extension inhibits the narrative self (Farb et al., 2007).

Secondly, mind-wandering has been shown to be negatively correlated with well-being in normal subjects in daily life. Intriguingly, it does not matter much what activity one is doing or whether the contents of the mind are subjectively pleasant or unpleasant - mind-wandering appears to cause a drop in well-being (Killingsworth & Gilbert, 2010). This might be counterintuitive since pleasant daydreaming during an unpleasant activity sounds like pleasant relief, however, Killingsworth and Gilbert (2010) found the opposite - that even pleasant mind-wandering is at best neutral.

The third observation is that when well-being is at its lowest, in patients with major depressive disorder (MDD), their minds have an increased tendency to wander in the form of depressive rumination. This chronic negative self-focus reduces the ability of depressed

individuals to engage in external attention (Belleau, Taubitz, & Larson, 2014) and to disengage from negative stimuli (Sheline et al., 2009).

Though Buddhist doctrine might have much to say about meditation the current hypothesis is mostly inspired by observations within the realm of science. A brain network that has gotten increasing attention for its role in thinking and selfhood is the default mode network (DMN; See Figure 1. And Figure 2.). The DMN is a network of brain areas that deactivate during external tasks and come online during rest (Raichle et al., 2001) and as such it initiates the familiar experience of mind-wandering and off-task thinking (Mason et al., 2007). Its activity is anti-correlated with external attention (Fox et al., 2005; Vanhaudenhuyse et al., 2011) and mostly self-referential or internally directed (Gusnard, Akbudak, Shulman, & Raichle, 2001; Spreng, Mar, & Kim, 2009). As such it is responsible for constructing the narrative self (Northoff & Bermpohl, 2004). The neuroscience of the DMN squares well with the common saying "I got lost in work" – externally directed attention is anti-correlated with the DMN. When losing oneself in work, at least momentarily, the "I" might literally get lost due to intense external attention. A loss of self resulting from concentration echoes what Buddhists are trying to achieve through meditation.

Activity in the DMN also relates to depression where it has a higher resting activity (Sheline et al., 2009; Zhu et al., 2012). Meditation on the other hand reduces activity in the network (Berkovich-Ohana, Glicksohn, & Goldstein, 2012; Fingelkurts, Fingelkurts & Kallio-Tamminen, 2016). Evidence in clinical trials show that meditation has an effect against depression when used as an intervention (Goyal et al., 2014) and reduces symptoms of depressive rumination (Ramel, Goldin, Carmona, & McQuaid, 2004). It is easy to imagine how

mindfulness meditation, which actively trains participants to let go of narrative thought, can have this effect.

The aim of this literature review is to investigate the relationship between well-being, mind-wandering, and self-referential processing, with an emphasis on its neural underpinning in the DMN. The hypothesis is that well-being is negatively correlated with mind-wandering, narrative self-reference and its neural correlates of DMN-activity. In order to test this claim the paper will examine DMN activity and narrative self-reference in three "levels" of function: normal function in daily life; in people with depression; and in meditators. Mind-wandering is expected to be high in depression where well-being is lowest. Conversely, meditation is expected to improve well-being and reduce mind-wandering. This relationship is expected to be mirrored by activity in the DMN. High DMN activity is believed to increase mind-wandering and decrease well-being, and vice-versa. Even if this relationship is more complex than existing on a simple spectrum of high- to low DMN activity with corresponding high to low wellbeing, at a minimum the same areas of the DMN are expected to display the mirror-opposite behaviour in depression as compared to meditation.

The Sense of Self

"Who am I?"

To find the fundamental essence of one's own identity has always been one of the great philosophical questions and has garnered many different answers throughout the times. Ancient examples range from the idea of the immortal soul in the Abrahamic traditions to Buddhism, where the doctrine of non-self (anattā), the explicit rejection of any permanent self, is regarded as one of the three marks of existence (Gombrich, 2018). Modern philosophy of mind and cognitive science has an equally impressive range of conceptions despite being constrained by empirical considerations. Strawson (1999) lists some of the almost comically numerous proposed selves:

...the cognitive self, the conceptual self, the contextualized self, the core self, the dialogic self, the ecological self, the embodied self, the emergent self, the empirical self, the existential self, the extended self, the fictional self, the full-grown self, the interpersonal self, the material self, the narrative self, the philosophical self, the physical self, the private self, the representational self, the rock bottom essential self, the semiotic self, the social self, the transparent self, and the verbal self ... (p. 100)

In other words there is a clear overabundance of terms. In addition, the terms used when discussing the self are both complex and ephemeral, which is further compounded by the use of different terminologies by different authors (Northoff et al., 2006; Prebble, Addis, & Tippett, 2013). Therefore neuroscience can provide a concrete point of reference to which these ethereal

terms can be anchored. Objective measurements from behaviour and neuroimaging can also serve to weed out terms which fail to explain the evidence.

The division of the self into narrative- and experiential self has support in both philosophy of mind and cognitive neuroscience (Farb et al., 2007; Gallagher, 2000; Lieberman, 2007). Many philosophical notions of the self can be collapsed into and divided between one of these two categories, including the many selves previously listed (Gallagher, 2000). The narrative self contends that we create coherent narratives about ourselves and the "self" is the character we place in the middle of this narrative. These narratives are what gives us a sense of identity that extends through time, from our personal past, through the present moment, and into the future (Gallagher, 2000; Prebble et al., 2013). The experiential self corresponds to conceptions of minimal selfhood that conceptualize the self as the immediate perceptual and somatosensory experience from the first person perspective. It is spatial, embodied, and lacks temporal extension beyond the current moment (Gallagher, 2000; Zahavi, 2011). The experiential self is often thought to be a prerequisite for the narrative self, and anteceding it in both phylogeny and ontogeny (Zahavi, 2011).

There are several key differences between the narrative and experiential self. Firstly, the division is made along a temporal axis, where the experiential self exists in the here and now and the narrative self is extended in time. Narrative self-reference is thought to maintain the sense of a personal identity that endures through time through a constant stream of self-related thinking. These thoughts form a self-narrative that links experiences together across time, binding the memories of who you were in the past with your imagined trajectory for the future (Farb et al., 2007; Gallagher, 2000; Lieberman, 2007; Northoff & Bermpohl, 2004).

The two selves are also different in content. Experiential self-reference is relatively spatial and physical since it consists of sensory input from the environment and the body.

Narrative self-reference is relatively mental, concerning processes such as thinking, memories, inner speech and mind-wandering (Farb et al., 2007). In the same way there is a difference in where the information originates. The informational content of the experiential self is exogenous since it enters awareness from outside the mind, even though this source can be within the own body. In narrative self-reference it is endogenous, since it is generated within the mind and brain (Lieberman, 2007; Spreng, 2012; Vanhaudenhuyse et al., 2011).

There are certainly philosophical nuances or distinctions that are lost by equivocating the many selves into two broad categories, however the goal is to have templates to which neuroscientific evidence can be measured against. In a similar vein the goal of this paper is not to pick sides in the philosophical debate about what "The Self" ultimately amounts to, but is content with noting that there are two main distinct forms of self-reference, which can be distinguished by their neural signatures (Farb et al., 2007). This is neither a search for The Self in the brain, it is an examination of how distinct forms of self-referential processes in the brain differentially impacts well-being. However, the emphasis of this paper is distinctly on the narrative self, which I in the next chapter will argue can be firmly located in the DMN.

The Default Mode Network

History

Even though the DMN has become one of the fastest growing neuroscientific research topics of the 2000s (Andrews-Hanna, 2012), its discovery was somewhat accidental (Buckner, Andrews-Hanna, & Schacter, 2008). During the 1990s several PET studies used resting as a control condition that they compared to the cognitive and perceptual tasks they were studying

(Buckner et al., 2008). Since the DMN becomes active during rest these experimenters unwittingly collected imaging data that would lead to the mapping of the DMN (Buckner et al., 2008). The need to understand resting as a control condition led researchers to reanalyse rest data from those previous studies and discover that the same areas of the brain consistently deactivated when participants switched from rest to engaging in a specific task (Raichle et al., 2001; Shulman et al., 1997) This pattern of activity was dubbed "the default mode of brain activity" since the brain to "defaults" back to it as soon as external demands on attention go down (Greicius, Krasnow, Reiss, & Menon, 2003).

Since the DMN was discovered in resting participants and deactivates during some tasks it is conceived of as only task-negative and therefore known as the Task-negative network (Spreng, 2012). That view does not paint the complete picture for two main reasons. Firstly, when the task at hand requires internally focused attention, such as during introspection, self-referential tasks, memory tasks, and emotional processing, the DMN is recruited (Andrews-Hanna, 2012; Schilbach et al., 2012; Spreng, 2012; Uddin, Iacoboni, Lange, & Keenan, 2007). Secondly, though a person may be at rest the brain is always at work. Curiously, the metabolism of the brain as a whole hardly increases during high demands on attention and cognition (Raichle, 2010). Instead of reducing activity when external demands on cognition go down, activity is subsumed by the DMN. So rather than constituting a passive state it is a highly active baseline that can be interrupted by external demands on conscious attention (Mason et al., 2007; Raichle, 2010).

Neuroanatomy of the DMN

Quite appropriately considering its role in internal awareness the DMN is mostly situated along the cortical midline, on the medial surfaces of the interhemispheric fissure (See Figure 1.).

The DMN consists most importantly of the medial prefrontal cortex (mPFC), the medial parietal cortex, especially the posterior cingulate cortex(PCC), as well as the inferior parietal lobules (IPL) (Greicius et al., 2003). The medial temporal lobe (MTL) plays a central role in the function of the DMN (Spreng et al., 2009), and the lateral temporal cortex (LTC; See Figure 2.) also has significance (Andrews-Hanna, Smallwood, & Spreng, 2014; Buckner et al., 2008). There are some less consistently reported areas suggested being minor parts of the DMN, such as the cerebellum by Fox et al. (2005); and visual areas by Christoff, Ream, and Gabrieli (2004). However, delving further into the heterogeneity of the DMN (e.g. Kernbach et al., 2018) serves no further purpose in the context of this paper.

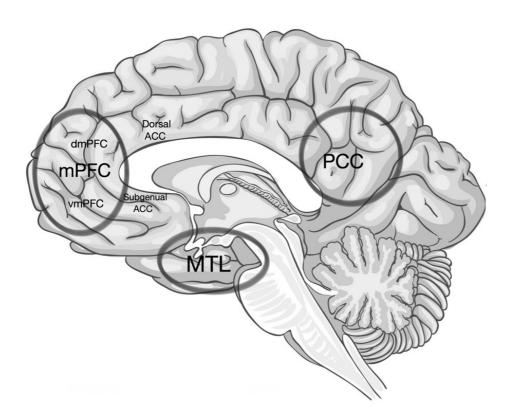


Figure 1. Medial view of the brain with DMN areas encircled (Adapted from Vasilisatsoy).

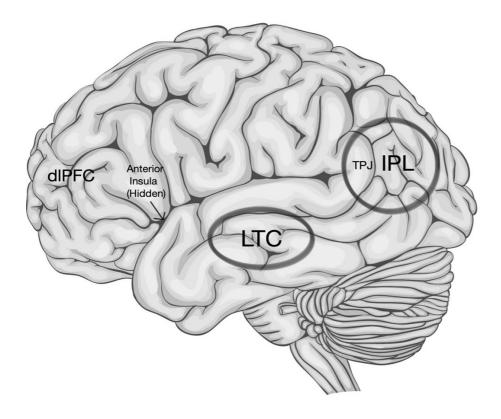


Figure 2. Lateral view of the brain with areas of the DMN encircled (Adapted from Vasilisatsoy).

Neuroscience operates under the general maxim that function follows form (Kristan & Katz, 2006). This is applicable to the DMN since its function as a network depends on the function of its constituent nodes. Each of these nodes contributes a part of the general function. Conversely, when seen as a whole the DMN reflects the summed characteristics of each of its nodes. However, wholes can have the somewhat awkward tendency to be more the sum of its parts, which in this case necessitates an examination of both the parts and the whole.

The DMN Core. The DMN consists of a core and two subsystems with partially different functions. The core consists of the mPFC and PCC, together with a lateral area that includes parts of the IPL, TPJ and angular gyri (Andrews-Hanna et al., 2014). The mPFC and

PCC are the most important hubs of the DMN, both showing the highest metabolism at rest (Greicius et al., 2003; Gusnard et al., 2001) as well as the most robust structural connectivity to each other in the form of white matter fibers (Greicius, Supekar, Menon, & Dougherty, 2009). Both of the subsystems converge on these major connecting hubs (Andrews-Hanna, 2012; Andrews-Hanna et al., 2014). The core of the DMN have the most general functions that are reflective of the DMN as a whole. It is involved in mind-wandering, self-referential processes, autobiographical memory, and evaluative processes, including emotional- and moral judgements (Andrews-Hanna et al., 2014).

The PCC is in addition to its default mode activity activated in a wide range of tasks with an emphasis on their relation to the self (Andrews-Hanna et al., 2014) as well as navigation from an egocentric perspective (Spreng et al., 2009). It is also especially important in tasks related to autobiographical memory, over and above the mPFC (Sestieri, Corbetta, Romani, & Shulman, 2011). A finding corroborated by white matter connections connecting the PCC and MTL (Greicius et al., 2009). Taken together these findings show that the PCC integrates information about the self within a context of space and time (Hamilton, Farmer, Fogelman, & Gotlib, 2015)

The mPFC is active during self-related processes, decision making, emotion, and social processing (Andrews-Hanna et al., 2014). The vmPFC is associated with evaluation and emotion. It activates both in response to moral judgements, selecting according to personal preference (Lieberman, 2007) and more concrete acts of evaluation such as during monetary transactions (Plassmann, O'doherty, & Rangel, 2007). It is also involved in ratings of emotional salience and self-relatedness (Phan et al., 2004). With its connections to both other cortical areas and limbic structures related to motivation the vmPFC is seen as integrating information to determine salience, emotion, reward and affective self-relevance (Andrews-Hanna et al., 2014).

The final component of the DMN core consists of an area encompassing the angular gyri, TPJ and IPL (Andrews-Hanna et al., 2014; Buckner et al., 2008). This area plays a part in a large number of tasks such as theory of mind, memory, semantic, and conceptual processes. Its role as a hub stems from its multiple connections integrating multiple sensory inputs with conceptual information into a spatio-temporal frame of reference (Andrews-Hanna et al., 2014; Buckner et al., 2008).

The function of these hubs are lateralized. The left IPL is more connected to the rest of the DMN at rest (Bellana, Liu, Anderson, Moscovitch, & Grady, 2016) and reacts stronger to instances of verbal self-description (Davey, Pujol, & Harrison, 2016). Considered apart from their roles in the DMN the left IPL is highly implicated in semantic processing together with the left LTC (Bonner, Peelle, Cook, & Grossman, 2013). The right IPL is important for the spatial relationship of the mind and body as evidenced by how electrical stimulation of the area produces out-of-body experiences (Blanke, Ortigue, Landis, & Seeck, 2002). This relationship also holds true in theory of mind reasoning where the left TPJ displays activity in a broad range of settings whereas the right TPJ is sensitive to the location of other persons in space (Abraham, Werning, Rakoczy, von Cramon, & Schubotz, 2008).

DMN Subsystems. In addition to the core the DMN has two subsystems. One is the MTL-subsystem which is important for memory and the other is the dmPFC subsystem which is important for theory of mind.

The MTL-subsystem consists of the MTL, the posterior IPL and the retrosplenial cortex (Andrews-Hanna et al., 2014). Considering that the MTL contains the hippocampus, well known for its role in memory (Scoville & Milner, 1957), it comes as no surprise that the MTL-subsystem manages the episodic memory functions of the DMN (Andrews-Hanna et al., 2014).

More than merely retrieving memories, the subsystem has increasingly become appreciated for its role in imagination and using stored memories in the construction of novel scenarios (Spreng & Andrews-Hanna, 2015). The high level of activity in the MTL during rest has led some to suggest that long-term memory forms the basis for spontaneous thought (Christoff et al., 2004). Furthermore, a study of the DMNs active functions, such as theory of mind, prospection and navigation showed that the MTL was the only area where all the tasks overlapped (Spreng et al., 2009).

The dmPFC-subsystem consists of the dmPFC, the LTC and the TPJ. The dmPFC and the TPJ are jointly well recognized for their role in theory of mind and reflecting about mental states of both self and other (Andrews-Hanna et al., 2014; Denny, Kober, Wager, & Ochsner, 2012). The TPJ together with the LTC, particularly on the left side, are associated with semantic and conceptual reasoning (Bonner et al., 2013). The dmPFC-subsystem is skewed, consisting of a much larger portion of the left TPJ and LTC than the right (Andrews-Hanna et al., 2014).

Interaction with other networks

The DMN can only be understood with reference to the other two large scale brain networks with which it interacts - the central executive network (CEN) and the salience network (SN)(Menon, 2011). They have been jointly characterized as "task-positive" in relation to the task-negative activity of the DMN (Fox et al., 2005; Spreng, 2012) and have also been referred to as the extrinsic mode network as opposed to the default mode network (Hugdahl, Raichle, Mitra, & Specht, 2015). Though they are jointly characterized as task-positive, the CEN and the SN are two separate networks with separate functions (Menon, 2011; Spreng, 2012).

The CEN can be seen as the opposite of the DMN. It is engaged during bouts of focused awareness and goal oriented problem solving (Hugdahl et al., 2015). It consists mainly of lateral

posterior parietal areas, lateral prefrontal areas, especially the dorsolateral prefrontal cortex (dlPFC; See Figure 2.), and secondary motor areas (Fox et al., 2005; Hugdahl et al., 2015; Spreng, 2012). External attention and activity in the CEN is anti-correlated with internal attention and activity in with the DMN. One or the other can be active but rarely both at the same time (Fox et al., 2005; Hugdahl et al., 2015; Spreng, 2012; Uddin, Clare Kelly, Biswal, Xavier Castellanos, & Milham, 2009; Vanhaudenhuyse et al., 2011). However the DMN has a stronger attenuating effect on the CEN, which leads to the DMN more easily disrupting externally focused attention than vice versa (Uddin et al., 2009). The higher the demands on attention the stronger this anti-correlation between the CEN and DMN becomes (Fox et al., 2005) which probably happens because both these networks compete for limited general-purpose cognitive resources (Dixon, Fox, & Christoff, 2014).

The interaction between the DMN and the CEN is mediated by the SN. The SN is neither internal nor external. Rather, it integrates and mediates between the two larger networks. It is important in orienting attention towards salient stimuli, integrating internal and external streams of information, and integrating bottom up information with top down control processes and goals (Menon & Uddin, 2010; Seeley et al., 2007). It consists of the dorsal ACC (See Figure 1.) and anterior insula (See Figure 2.) (Seeley et al., 2007). The anterior insula, especially on the right side, has been implicated both in interoceptive awareness (Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004) and for its role in switching between the DMN and the CEN (Sridharan, Levitin, & Menon, 2008). The dorsal ACC is an important area for detecting conflict in incoming streams of information (Botvinick, Cohen, & Carter, 2004) and focus attention away from distraction and towards relevant information in order to accomplish the task at hand (Weissman, Gopalakrishnan, Hazlett, & Woldorff, 2005).

Functions of the DMN

After looking at the parts and subcomponents of the DMN it is time to look at the function of the network as a whole. As previously stated the high "resting" metabolism of the DMN reflects its role in self-generated or spontaneous cognition, which has been demonstrated by several studies (Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015; Mason et al., 2007). This spontaneous cognition is commonly known and experienced as mindwandering, reflecting how the mind at rest does not just go blank, but is filled with thoughts, fantasies and memories (Smallwood & Schooler, 2006).

Mason et al. (2007) showed how mind-wandering and DMN activity were correlated by using brain imaging and thought sampling. In two conditions participants could solve either a task that they had practiced and had become familiar with, or a functionally equivalent task that was new to them. Mason et al. (2007) found that both mind-wandering and DMN activity was highest during the practiced tasks, which required less conscious attention to complete.

Additionally, mind-wandering could be predicted by the difference in DMN activity between the novel and the learned task. This experiment also shows how DMN activity and mind-wandering not only happen during rest but also interrupts active efforts to complete external tasks, especially those that require little conscious effort (Mason et al., 2007).

In addition to its role in mind-wandering during rest, the DMN plays an important role in active processes. The DMN is activated in a wide array of tasks, in domains such as autobiographical memory, prospection, self-representation, social processing, navigation, and evaluation (Andrews-Hanna, 2012; Andrews-Hanna et al., 2014; Buckner & Carroll, 2007; Schilbach et al., 2012; Spreng, 2012; Uddin, et al., 2007). Though seemingly disparate these

abilities might share the common denominator of shifting attention inward and use information stored in long-term memory combined with mental models to imagine times, places and perspectives other than our own in the here and now (Andrews-Hanna et al., 2014; Buckner & Carroll, 2007; Christoff et al., 2004; Gusnard, 2005).

The ability to imagine future scenarios and plan behaviour is thought to be one of the primary benefits granted by the DMN (Andrews-Hanna, 2012; Gusnard, 2005). It is therefore not surprising that the MTL with its role in simulation and prospection is centrally involved in mindwandering during the resting state (Andrews-Hanna, 2012; Christoff et al., 2004). Andrews-Hanna et al. (2010) found that participants at rest in an fMRI scanner spent about half of their time engaged in mental time travel, thinking about the past or the future. This mental time travel was skewed toward the future, especially the immediate future since 84% of temporal thinking was about the rest of the day and the tomorrow. This is in line with other studies that suggests that the DMN spontaneously initiates mental time-travel to serve the adaptive function of preparation for the personal future, for example by simulating possible scenarios and putting plans in order (Andrews-Hanna, 2012; Baird, Smallwood, & Schooler, 2011).

Evolution of the DMN

The involvement of the DMN in all these different areas, self-awareness, mind-wandering and internal cognitive processes connects to its evolution. It is believed that the DMN evolved as a mechanism for integrating external stimuli with internal information, such as goals and memories, in order to react flexibly to the environment (Gusnard, 2005). Simpler animals react to the environment in a stereotypical stimulus-response fashion. As brains grew more complex they evolved the capacity for planned behaviour and flexible responses to different situations. This required a system for disengaging attention from the immediate external environment in

order to limit its direct control so that internal sources could exert a greater influence. These internal sources are for example goals, evaluations, memories of past events, and representations of the self. Integrating this information with external information allows for maximizing the impact of actions to accomplish the current goals of the organism (Gusnard, 2005).

The deeper function of the DMN in the brain is as a system for internally directed attention and carry out internal cognitive processes (Schilbach et al., 2012; Vanhaudenhuyse et al., 2011). The introspective capacity of the DMN runs deeper than the explicit, psychological representations of the self. Under this view the DMN is the very system that allows the brain to access its own current state and to represent itself (Gusnard, 2005; Gusnard et al., 2001; Schilbach et al., 2012). The idea that the DMN plays this fundamental role in the brain is elaborated on by Vanhaudenhuyse et al. (2011) who write:

...the pervasiveness of the default network after general anesthesia in monkeys, in vegetative state (only cortico-cortical connectivity), and its absence in brain death, reflects a fundamental intrinsic property of the brain's organization that seems to transcend the levels of consciousness. (p.576).

This idea can explain why there is an overlap between areas processing memory, mentalizing, and evaluation. It also explains why these areas spontaneously activate in the absence of salient external stimuli. Under this framework the spontaneous activation of these internally directed self-referential functions serves the purpose of planning behaviour and aligning it with the organisms goals. In addition, the regions comprising the DMN are among the

areas that have undergone the most change between monkey and human (Gusnard, 2005).

Perhaps this is the basis for the unique human self-awareness and capacity for self-reflection.

The Narrative Self in the DMN

What is then the relationship between the DMN and the narrative self? Does the DMN and the processes it mediates play a special role in underpinning narrative forms of selfreference? One of the chief defining features of the narrative self is extension in time (Gallagher, 2000). The extension of the self in time is conspicuously resembling to mental time-travel - the somewhat counterintuitive idea that remembering one's past and imagining one's future constitute one single capacity (Buckner & Carroll, 2007; Schacter, Addis, & Buckner, 2007; Suddendorf & Corballis, 2007). This capacity, which includes both episodic memory and prospection, is specifically related to the past and future of the self. A point which is illuminated by how MTL lesion patients can retain a general concept of the future but not envision their own personal future. These deficits in prospection are proportional to their deficits in autobiographical memory which further suggests that mental time-travel is responsible for extension of the self in time (Buckner & Carroll, 2007). Mental time-travel crucially engages the MTL-subsystem of the DMN (Andrews-Hanna et al., 2014; Buckner & Carroll, 2007; Schacter et al., 2007) and the ability to imagine future scenarios and plan behaviour is thought to be one of the primary benefits granted by the DMN (Andrews-Hanna, 2012; Gusnard, 2005). It is therefore of little surprise that the mental time-travel and the MTL are centrally involved in mind-wandering during the resting state (Andrews-Hanna et al., 2010; Andrews-Hanna, 2012; Christoff et al., 2004). Autobiographical memory is also theorized to be a prerequisite for the sense of phenomenological continuity where especially its semantic forms are responsible in representing an objective self extended in time and creating a life-narrative (Prebble et al., 2013). The brain

might create a self to help in organizing memory into a coherent life story (Fivush, Haden, & Adam, 1995) where it can serve as a centre of narrative gravity (Dennett, 1993; Gallagher, 2000). Taken together this evidence supports that the extension of the self in time and the 'once upon a time' of our life story relies on the MTL-subsystem of the DMN.

Narrative identity contends that the self is the story we tell ourselves about our lives and who we are, making the self both the narrator and protagonist (McAdams & Zapata-Gietl, 2015). Investigating the metaphor of identity as a narrative reveals an interesting convergence of the elements of a narrative and the functions of the DMN. A narrative takes the shape of a linguistically mediated drama, with a setting in time and space, with characters that carry out plots in accordance to their motives (McAdams, 2001; McAdams & Zapata-Gietl, 2015). This meshes well with the theorized unifying feature of the DMN, simulating scenarios of times, places and perspectives other than our own in the here and now (Buckner & Carroll, 2007). Another proposed grand function of the DMN that makes it a prime stage for the life story to unfold is internal scene construction (Hassabis & Maguire, 2007). The very act of engaging in a narrative comprehension and production engages the dmPFC (Andrews-Hanna et al., 2014). Probably due to narratives engaging the networks capacity for theory of mind reasoning (Spreng et al., 2009), taking the spatial perspective of others (Mano, Harada, Sugiura, Saito, & Sadato, 2009) reasoning about mental states (Gweon, Dodell-Feder, Bedny, & Saxe, 2012) and language and conceptual reasoning (Andrews-Hanna et al., 2014). A final area that has an interesting relation to narratives is the vmPFC which is important in the attribution of good and bad, as evidenced by its broad role in moral reasoning, emotions, and evaluation (Amodio & Frith, 2006).

One of the questions this essay set out to answer is the relationship between being present and the self and its neural implementation. The DMN mediates self-awareness on several levels that are commensurate with narrative self-reference and antithetical to being here and now. Its role in mind-wandering is a process of turning attention inward towards internally generated content and (at least sometimes) reflects a failure to engage in external attention (McVay & Kane, 2010). Awareness of internal and mental processes mediated by midline areas are anticorrelated with bodily and external awareness and lateral areas (Vanhaudenhuyse et al., 2011). The DMN is also responsible for psychological self-referential activity as accessing stored selfknowledge (Ochsner et al., 2005) and introspecting about one's mental state (Ochsner et al., 2004). In addition, when Farb et al. (2007) directly compared focus on direct experience versus narrative self-focus a focus on the immediate experience led to decreased activity in the mPFC. This is matched by the at the time surprising finding that self-reflection activates medial frontoparietal areas whereas self-recognition and agency judgement activated lateral frontoparietal areas (Lieberman, 2007). In a meta-analysis of the relationship between the self and the DMN Oin and Northoff (2011) found that the direct overlap of self-referential and default activity in the mPFC suggests that the sense of self is a result of resting state- and stimulus induced processes. The question posed about being present and the self can thus be answered that the narrative self-referential activity is mediated by the DMN and is the opposite pole of the experiential awareness and the neural systems it is mediated by.

Mind-Wandering and Well-Being

The idea that mind-wandering is negatively correlated with well-being is supported by multiple studies using different methodologies (Andrews-Hanna et al., 2013; Killingsworth & Gilbert, 2010; Poerio, Totterdell, & Miles, 2013; Song & Wang, 2012; Stawarczyk, Majerus, Van

der Linden, & D'Argembeau, 2012). Initial evidence suggested that mind-wandering in and of itself always had a net negative effect on affect, regardless whether its content was positive or negative (Killingsworth & Gilbert, 2010), however later studies have put that into question.

The now famous study by Killingsworth and Gilbert (2010) used a telephone app to gather an unprecedented volume of data in an ecologically valid setting whilst also avoiding the problems with retrospective self-reports. Participants' state of mind were sampled several times a day and were asked three things. What they were currently doing, how they were feeling and whether they were mind-wandering. They were also asked to rate if the current activity and contents of mind were experienced as positive, negative, or neutral.

The study had several interesting findings. Participants were on average mind-wandering about half of the time (46.9%). Whether participants were working, exercising, or taking care of children, no activity had mind-wandering dropping lower than 30%. Not even when they were meditating or praying. There was however one single glaring exception. Making love. The content of mind-wandering was mostly positive, however, even during the least enjoyable activities mind-wandering was not associated with better mood. At best the effect of mind-wandering was neutral. A time-lag analysis showed that mind wandering preceded unhappiness, suggesting that mind wandering led to unhappiness and not the other way around. Therefore the idea that mind-wandering gives rise to negative mood saw strong initial evidence.

However, the case might not be so clear cut. First of all, since participants were probed at most three times a day the time between probes could be several hours. It is hard to believe that a single instance of mind-wandering can lower affect several hours later. Two subsequent studies using similar methodology but shorter time between probes have failed to replicate the results (Poerio et al., 2013; Song & Wang, 2012). The study by Poerio et al. (2013) also used a

telephone app to sample experiences of mood and mind-wandering. Whereas the time between probes in the Killingsworth and Gilbert (2010) study could be several hours, Poerio et al. (2013) sampled contents of mind with 15 minute intervals. In contrast to Killingsworth and Gilbert (2010), Poerio et al. (2013) did not find that mind-wandering directly affected mood, rather, the affective valence of mind-wandering episodes were a direct result of what mood participants had been 15 minutes earlier. Another finding from Poerio et al. (2013) was that sadness predicted retrospective mind-wandering whereas anxiety predicted increased prospective mind-wandering. Corroborating the picture that it is emotion that induces mind-wandering is a study by Smallwood, Fitzgerald, Miles, and Phillips (2009) which showed that provoking negative affect in participants will cause their minds to wander to a higher degree. A later study also showed that a bad mood will shift mind-wandering towards the past (Smallwood & O'Connor, 2011). It is entirely possible that the study by Killingsworth and Gilbert (2010) failed to rule out that negative moods caused mind-wandering.

As argued by Mason, Brown, Mar, & Smallwood (2013) there are also several other confounding 'third' factors that might cause both the negative mood and the mind-wandering. First, it might simply reflect that participants were engaged in boring tasks. Minds wander to a higher extent when doing tasks that are neither novel nor challenging (Mason et al., 2007). Mindwandering is known to be attuned when tasks include a monetary reward, reflecting its sensitivity to how motivated one is to do the task (Esterman et al., 2016). Thus, engagement in a less than motivating or boring task is a credible alternative explanation for the correlation. Secondly, it could reflect some sort of difficulty that participants were facing in their life. Whilst mind-wandering, people often reflect upon goals that they have committed to but not yet fulfilled. Especially when there are difficulties in achieving this goal (Mason et al., 2013). Other

worries could also cause the mind to wander. Antrobus, Singer and Greenberg demonstrated this in their 1966 study where participants were exposed to fake news recordings about serious escalations in the ongoing Vietnam war. Quite predictably this increased both spontaneous thinking and negative affect. A third source of the correlation could be traits within the participants themselves. Depressive symptoms is a known source of both increased mindwandering and negative affect (Hamilton et al., 2015). An effect shared with neurotic and anxious traits (Mason et al., 2013). Furthermore, deficits in attention might exacerbate the connection since it implies an inability to become engaged, leading to boredom (Cheyne, Carriere, & Smilek, 2006) and is in itself related to depression (Carriere, Cheyne, & Smilek, 2008).

Even though mind-wandering is correlated with lower affect, which is actually further demonstrated by these examples, it is not obvious that mind-wandering is the cause. What was so surprising about the Killingsworth and Gilbert (2010) study (and commensurate with meditation as a means of psycho-spiritual liberation) was that self-generated thoughts were so consistently detrimental. In contrast to the rather bleak conclusion of Killingsworth and Gilbert (2010), that positive thoughts had at best a neutral impact, Andrews-Hanna et al. (2013) found that thoughts that were positive, specific, future oriented, and less personally significant were in fact conducive to emotional wellbeing. Similarly Ruby, Smallwood, Engen, and Singer, (2013a) found that thoughts related to the future led to subsequent improvements in mood. It seems that the most negative effects of mind-wandering occur in those that are predisposed to negative affect. In these individuals incidents of task unrelated thoughts appear to increase later access to negative associations and thus have a causal effect on negative mood (Marchetti, Koster, & De Raedt, 2012a).

In summary, mind-wandering does not appear to cause dysphoria for most people most of the time. This is good news given how we spend half of our waking time lost in thought (Andrews-Hanna et al., 2013; Killingsworth & Gilbert, 2010). Considering the sheer ubiquity of the phenomenon it is almost inconceivable that it could be so damaging. Though there is a strong correlation between the two (Mason et al., 2013), the causal effect mind-wandering has in lowering mood is probably dependent on its phenomenological content (Andrews-Hanna et al., 2013). Mind-wandering also has tangible benefits. Besides its main job of planning for the future (Baird et al., 2011) it can improve creative problem solving (Baird et al., 2012) and delaying gratification (Smallwood et al., 2013). The advantage of mind-wandering is nicely summarized by Smallwood, Ruby and Singer (2013): "Although immersion in the here and now is undeniably advantageous, under appropriate conditions the capacity to let go of the present and consider more pertinent personal goals may have its own rewards". In other words, not all minds that wander are lost (Smallwood & Andrews-Hanna, 2013). However, mind-wandering is not as benign in depression as we shall see next.

Depression

Depression is a mood disorder characterized by persistent low affect. It has been recognized since antiquity and scientifically investigated for more than a century. Nevertheless, its basis in the brain is not fully understood (Holtzheimer & Mayberg, 2011). This has serious implications since it leads to drastic reductions in quality of life (Sobocki et al., 2007a) combined with a high prevalence (estimated 20-35% lifetime prevalence in Sweden; Sobocki et al., 2007b) makes it a leading cause of disability worldwide (World Health Organization, 2008). Despite lacking an agreed upon neurobiological framework there is emerging evidence of the involvement of several attention- and mood- regulating areas, many of which are part of the

DMN. Additionally many of the hallmark cognitive deficits displayed in depression take place in processes mediated by the DMN (Marchetti, Koster, Sonuga-Barke, & De Raedt, 2012b).

Depression, at least as a transient state of lower mood, can arise due to a host of different causes ranging from infection to stress. Since it can be induced by such a wide array of causes the depressive state in and of itself might be best conceptualized as a nonspecific, general response. Perhaps originally serving an adaptive function that evolved to withdraw from danger (Gilbert, 2006). Depression has broad effects in cognitive, emotional and somatic systems.

Therefore, as Holtzheimer and Mayberg (2011) argue, depression clinical disorder should not be defined as the negative moods per se but the tendency to inappropriately enter into them and an inability to shift away from them. This definition places more emphasis on relapse, since depression often is recurrent and more so after each episode. It also has implications for treatment which rarely are universally effective and many antidepressants "can shift a patient out of the depressive state but may not necessarily prevent re-entry into that state." (Holtzheimer & Mayberg, 2011, p. 8). Therefore a good definition of depression can explain both the core psychological symptoms and the tendency for relapse.

Rumination

What role does then self-related processes and DMN activity play in depression, considering the logic outlined above? A good place to start the examination is rumination. It is one of the crucial cognitive risk factors in developing depression and in its recurrence (Marchetti et al., 2012b). Rumination consists of persistent negative self-focused thoughts, usually centred around the depression, the negative mood, and its consequences (Nolen-Hoeksema, 2000). It predicts recurrence of depression in remitted individuals and remaining depressed even after accounting for the original severity of symptoms (Kuehner & Weber, 1999). In addition it

predicts depression in never depressed individuals (Nolen-Hoeksema, 2000) and even whether someone has ever been depressed (Hamilton et al., 2015).

The DMN in Depression

Several studies suggest that rumination is connected to alterations in the DMN and its interaction with task positive networks (Belleau et al., 2014; Hamilton et al., 2015; Marchetti et al., 2012b). The DMN becomes dominant over task positive areas though not in a way that implies a heightened level of activity of the DMN as a whole, all of the time. More precisely the DMN overpowers the task-positive networks in such a way that depressed individuals have a reduced ability to engage in external tasks, rather than the DMN being set to overdrive at baseline (Belleau et al., 2014; Marchetti et al., 2012b). Depressed individuals also have a stronger reaction to, and an impaired ability to disengage from negative thoughts and emotions, which is also reflected in their DMN-activity (Sheline et al., 2009).

In a healthy brain the DMN engages during rest but shuts it down in response to external demands on attention, when task-positive networks activate. Depressed individuals have trouble shutting the DMN down during external tasks where it shows persistent levels of activity, and task positive networks show deficient levels of activity (Marchetti et al., 2012b). This relationship likely mediates both the inability to shift away from self-related processing and the attentional deficits in external tasks that are displayed in depression (Belleau et al., 2014). Furthermore, rumination mediates between the attentional deficits seen in depression and the severity of depressive symptoms (Demeyer, De Lissnyder, Koster, & De Raedt, 2012). The imbalance of DMN to task positive areas is related to changes in the right fronto-insular cortex (Hamilton et al., 2011). This probably because the area switches between DMN and the CEN

(Sridharan, et al., 2008) but possibly reflects an increased detection of anxious body states that further decreases negative affect (Paulus & Stein, 2006).

An area that has been consistently implicated in depression is the subgenual ACC (See Figure 1.) (Berman et al., 2011; Greicius et al., 2007; Hamilton et al., 2015). The area is associated with behavioural withdrawal (Yang et al., 2009) and activates in response to peer rejection (Masten et al., 2011) The area is believed to act as an opposite pole to the dorsal ACC which engages in more positive and energetic behaviour (Hamilton et al., 2015). The area also activates in response to induced negative rumination, though to a higher extent when participants are instructed to feel the emotions rather than accepting them (Kross, Davidson, Weber, & Ochsner, 2009). In depression the subgenual ACC becomes integrated as a node of the DMN and its coactivation during rest likely reflects depressive brooding (Berman et al., 2011).

These two features of the DMN explains how rumination is persistent and negatively biased. The resting state is laden with the negative affect of the subgenual ACC whereas the persistence of rumination is related to persistence of DMN activity. A feature that also explains attentional deficits that are central to depression (Marchetti et al., 2012b). According to the 'impaired disengagement hypothesis' deficient activity of task positive areas reflects a failure of cognitive areas such as the dlPFC to down-regulate emotional limbic areas such as the amygdala. The same deficits in attention and cognitive regulation lead to persistent ruminative mindwandering that maintains negative affect (De Raedt & Koster, 2010; Koster, De Lissnyder, Derakshan, & De Raedt, 2011; Marchetti et al., 2012b). However the inverse has also been suggested, that limbic emotional areas essentially 'hijack' the DMN and higher cognition through the paralimbic areas including the subgenual ACC, the vmPFC, and insula (Northoff, Wiebking, Feinberg, & Panksepp, 2011). In summary, negative self-related processing and dominance of the

DMN is related both to the onset and severity of depression. Crucially, both attentional deficits and DMN dominance is still observable in individuals remitted from MDD, the level of which predisposes them to further depressive episodes (Demeyer et al., 2012; Marchetti et al., 2012b)

Meditation

Meditation as a concept denotes a wide range of techniques with the common denominator that they in some way use focused attention. Therefore this paper uses the term meditation to mean mindfulness-meditation, defined in the words of Jon Kabat-Zinn (2003) as "paying attention on purpose, in the present moment, and nonjudgmentally to the unfolding of experience moment by moment." (p.145). During meditation there is also an emphasis on avoiding getting caught in a stream of conceptual thought, in favour of focus on bodily and sensory experience, especially the breath (Hölzel et al., 2011). There is however a distinction between mindfulness meditation and state mindfulness, the state of mind which the practice aims to cultivate, and trait mindfulness, referring to an individual's tendency to be mindful over a longer period of time (Brown & Ryan, 2003).

Simply looking at this definition of meditation suggests how it could attenuate the DMN. Firstly purposefully paying attention is conceptually opposite of mind-wandering. A relationship that holds true in the brain, where focused attention is associated with activity in the extrinsic mode network regardless of whether the activity is internal or external (Hugdahl et al., 2015), and anticorrelated with the DMN (Fox et al., 2005). Focus on the present moment is contrary to mental time travel and on the immediate surroundings rather than internally constructed scenery. Attention is weighted towards external, especially somatosensory, sources rather than the internal sources which engage many DMN areas (Vanhaudenhuyse et al., 2011). Being non-judgmental is of course contrary to the judging and evaluating activity of the DMN and the vmPFC.

Neural Correlates of Meditation

Meditation is associated with a number of changes in the DMN. Both during active meditation as well as passively during the resting state in highly experienced meditators (Brewer et al., 2011). Brewer et al. (2011) compared highly experienced meditators to novices and found that the experienced meditators displayed both lower levels of mind-wandering during meditation, and lower activity in the PCC and the mPFC, the core hubs of the DMN. This supports the hypothesis that meditation reduces mind-wandering through reduced activity of the DMN. Highly experienced meditators also showed a higher degree of functional connectivity between the PCC and the dorsal ACC and the dlPFC both during meditation and at rest, areas related to working memory and task monitoring. Similarly, Lazar et al. (2005) found that highly experienced meditators had increased cortical thickness in areas related to cognitive control and attention, especially the right anterior insula and right dlPFC, as well as somatosensory and auditory areas.

Taken together these findings fit well with the view that meditation increases capacity to disengage from passive mind-wandering through maintained efforts of concentration to reallocate attention towards immediate perception of the body or environment. Both the study by Brewer et al. (2011) and Lazar et al. (2005) implicated the right dlPFC, which is important in working memory (Greicius et al., 2003) and is associated with external awareness (Vanhaudenhuyse et al., 2011), and being "on task" (Fox et al., 2005; Hugdahl et al., 2015). The right anterior insula, in which Lazar et al. (2005) found the highest increase in thickness, has been specially implicated both in interoceptive awareness (Critchley et al., 2004) and for its role in switching between the DMN and the CEN (Sridharan et al., 2008), as well its abnormal activity in depression being tied to a higher degree of DMN-dominance and levels of rumination

(Hamilton et al., 2011). The dorsal ACC which was implicated in the study by Brewer et al. (2011) is an important area for detecting conflict in incoming streams of information (Botvinick et al., 2004) and focus attention away from distraction and towards relevant information in order to accomplish the task at hand (Weissman et al., 2005).

Meditation and Self-Awareness

Farb et al., 2007 examined how an 8 week course in mindfulness could affect self-awareness. Farb et al., (2007) asked participants to read trait-related adjectives while in an fMRI scanner and either reflect on how it described them personally (narrative focus), or to monitor their immediate experience and reaction to reading the adjective (experiential focus). Farb et al. (2007) found that in both groups narrative focus activated the PCC and the mPFC, the DMN core, whereas experiential focus activated the posterior parietal cortex and the lateral prefrontal cortex, both areas of the CEN (Hugdahl et al., 2015).

There were also significant differences between the groups during the both conditions. During experiential focus the meditation group displayed reductions in both dorsal and ventral mPFC whereas the reductions in the novice groups corresponded to the subgenual ACC and the PCC and only to a smaller extent the mPFC. For novices activity during experiential focus rose most notably in left dlPFC and the posterior parietal cortices. In the meditation group on the other hand activity rose in right side lateral areas, being the right lateral prefrontal cortex (IPFC) the right insula and an area centred on the right IPL and surrounding secondary somatosensory region. The authors interpreted the higher activation of left IPFC and PPC in the novice group to indicate that experiential focus required more effort in fending off mind-wandering rather than being indicative of being truly present. This is also consistent with their relatively higher mPFC activity. Functional connectivity analysis of the meditation group showed the right insula

becoming decoupled with the vmPFC and instead becoming coupled with the lPFC. This was interpreted as that the viscerosomatic activity of the right insula, rather than being interpreted in the emotional and narrative lens of the vmPFC being more objectively experienced as transient bodily states through the lPFC.

Taylor et al. (2013) wanted to examine whether the findings of Farb et al. (2007) extended to meditators with more experience. In their study they compared the resting state functional connectivity within the nodes of the DMN in meditators with over 1000 hours of practice to novices with only 1 week of training. The intrinsic functional connectivity of the mPFC was expected to be lower in the novice compared to the meditator group. This relationship was realized with one area being the exception - the right IPL. Whereas several DMN nodes showed stronger interconnection in the novice group, only the right IPL showed stronger connections in the meditator group. The meditation group were responsible for all of the strengthened connections emerging from the right IPL. Taylor et al. (2013) believe that the meditators stronger right than left IPL connectivity reflects increased spatial awareness and decreased verbal self-referential processing. This is consistent with findings showing that self-referential processing lowered the connectivity between the right IPL and the PCC (van Buuren, Gladwin, Zandbelt, Kahn, & Vink, 2010). Taylor et al., (2013) also speculate that their findings reflect meditators having higher awareness of the present moment.

Meditation and the DMN

All of these studies (Brewer et al., 2011; Farb et al., 2007; Lazar et al., 2005; Taylor et al., 2013) use different measures, either activity and functional connectivity (Brewer et al., 2011; Farb et al., 2007), cortical thickness (Lazar et al., 2005), or resting state functional connectivity (Taylor et al., 2013). The studies were performed in different settings, rest (Taylor et al., 2013).

meditation (Brewer et al., 2011) and self-awareness tasks (Farb et al., 2007) and in participants with different levels of meditation training. However they all present converging evidence for the effect of meditation on the DMN. Taken together these findings fit well with the view that meditation increases the capacity to disengage from the passive mind-wandering and self-related processing of the DMN by through maintained efforts of concentration and shifts attention towards immediate perception of the body or environment. In neural terms this corresponds roughly to the SN reallocating activity from the DMN towards the CEN and away from self-generated activity towards task-positive and extrinsic activity.

The most consistent areas to show decreased activity and during meditation was the core of the DMN, the mPFC and the PCC. They showed lower activity during meditation in Brewer et al. (2011) as well as during experiential focus in Farb et al. (2007). In the Taylor et al. (2013) study a weaker resting state functional connectivity between the vmPFC and dmPFC was the only correlation that was predicted by hours of meditation practice. There were also several areas where meditators had increased activity and interconnection, almost all of them right lateralized. Both the study by Brewer et al. (2011) Lazar et al. (2005) and Farb et al. (2007) implicated the dlPFC, especially on the right side. It is an important area for working memory (Greicius et al., 2003), is associated with external awareness (Vanhaudenhuyse et al., 2011), and being "on task" (Fox et al., 2005; Hugdahl et al., 2015).

Another area of particular importance is the right insula in which meditators showed increased cortical thickness in the Lazar et al. (2005) study as well as showing increased engagement during experiential focus in meditators in the study by Farb et al. (2007). The right insula has been specially implicated both in interoceptive awareness (Critchley et al., 2004) and for its role in switching between the DMN and the CEN (Sridharan et al., 2008). Farb et al.

(2007) found a decoupling of the right insula and the vmPFC in meditators which might signify the decoupling of interoceptive insular activity with evaluative end emotional vmPFC activity and allow for "cooler" and more objective interpretation of visceral events.

An area that was found to have increased resting state connectivity to many other DMN-nodes by Taylor et al. (2013) and one of the areas which meditation-trained participants could recruit to a higher degree during the experiential condition in the Farb et al. (2007) study is the right IPL. Though not mentioned by Brewer et al. (2011) it can be seen in the supplementary material. As previously mentioned this finding likely signifies increased spatial awareness (Taylor et al., 2013)

Meditation against Depression

The aim of this paper is to investigate whether the narrative self-referential processes of the DMN serve a special role in mediating depression and whether a reduction of these processes are responsible for the benefits of meditation. Therefore a key question is if and how meditation works against depression? A large body of evidence supports the use of meditation against depression. A meta-analysis by Goyal et al. (2014) found that meditation is moderately effective as a clinical intervention used against depression. Similar though not better than other active treatments (Goyal et al., 2014). A meta-analysis by Piet and Hougaard (2011) found that mindfulness based cognitive therapy was effective in the prevention of recurrence though only in those that had already had more than two previous episodes. A meta-analysis on mindfulness based stress-reduction in healthy individuals saw reductions in depressive and anxious symptoms and that this effect was correlated with increases in mindfulness and compassion (Khoury, Sharma, Rush, & Fournier, 2015). In a study by Jain et al. (2007) students with distress were randomly assigned to either a 1-month meditation course or somatic relaxation. Though students

in both groups experienced decreases in distress and increases in psychological well-being the meditation group also experienced reductions in ruminative and distractive thoughts (Jain et al., 2007). The reduction of rumination after mindfulness based cognitive therapy in formerly depressed individuals serve as a predictor of recurrence even after controlling for residual depressive symptoms (Michalak, Hölz, & Teismann, 2011)

Mechanisms of Action

There are several proposed reasons as to why mindfulness meditation is effective against depression. The first mechanism is that meditation increases cognitive control and the capacity for emotional regulation. Depression has been characterized as an inability to cognitively downregulate negative cognition and emotion. Naturally this is translates to deficient activity in the task positive network, especially the dlPFC, and higher activity the DMN, especially the paralimbic areas such as the vmPFC including the subgenual ACC (Koster et al., 2011; Marchetti et al., 2012b; Northoff et al., 2011). Consistent with this view is the finding that lesions in the dlPCF predispose individuals towards depression whereas lesions in the vmPFC has a protective effect (Koenigs & Grafman, 2009). It also might be related to how the ACC, but not other somatosensory cortex, processes the affective component of pain (Rainville et al., 1997). The right dlPCF is one of the areas where activity most consistently increases due to meditation. Meditation also reduces activity in the DMN and the vmPFC (Brewer et al., 2011; Farb et al., 2007). This appears to occur through an increase in the SN areas dorsal ACC and the anterior insula (Farb et al., 2007; Lazar et al., 2005).

A second reason is that decreases emotional reactivity, an associated risk factor in depression (Marchetti et al., 2012b). Meditation has also been shown to increase emotional non-reactivity towards negative stimuli specifically through modulating activity in the insula (Paul,

Stanton, Greeson, Smoski, & Wang, 2013). Paul et al. (2013) suggest that participants with meditation training might be using interoceptive awareness to decrease emotional reactivity. Corroborating this view is that abnormal insular activity in depression is tied to a higher degree of DMN-dominance and levels of rumination (Hamilton et al., 2011) Interoceptive awareness can increase empathy (Ernst, Northoff, Böker, Seifritz, & Grimm, 2013) which could be a mechanism in promoting prosocial behaviour which is important in building eudaimonic well-being (Garland, Farb, Goldin, & Fredrickson, 2015). In accordance with the basic premise of this paper, it appears that narrative self-reference and DMN activity is counteracted by an increased reliance on the bodily awareness associated with experiential self-reference and task positive areas.

Though meditation is usually conceptualized as a cognitive exercise where the goal is to decrease thought it also encompasses emotional training. This process is thought to be a result from a combination of positive reappraisal and non-appraisal of aversive experiences (Hölzel et al., 2011). Positive reappraisal occurs when a challenging experience is reinterpreted in a positive light, either as being essentially harmless or even a positive experience which can be learned from. Non-appraisal occurs when accepting whatever one is feeling as passing mental events and observing them rather than reacting instinctively. When a negative emotion is allowed rather than suppressed this leads to exposure and eventually extinction and a reversal of fear conditioning (Hölzel et al., 2011). These processes are thought to both increase emotional well-being and capacity for emotional self-regulation (Hölzel et al., 2011). In a study by Paul et al. (2013) which examined the effect of mindful breathing on stress induction showed that the key aspect of the mindfulness construct that mediated the positive effect of mindful breathing was non-reactivity to inner experience. This reduced both rumination and negativity bias.

Discussion

The hypothesis of this thesis is that the narrative self-referential activity of the DMN is conflicting to well-being. This hypothesis was based on the findings of Killingsworth and Gilbert (2010), combined with the observations that mind-wandering goes rampant during depression, and that meditation increases well-being through a cessation of mind-wandering. Under this view the negative affective cost of mind-wandering comes from its role in goal directed prospection. The DMN is thought to use long-term memory to draw lessons from the past and generate plans for the future in order to accomplish personal goals (Andrews-Hanna, 2012; Gusnard, 2005). Though this serves a highly adaptive function, the dynamics of goal pursuit are such that a goal per definition is unfulfilled. Per definition, as soon as a goal is completed it is no longer a goal but a past achievement. In order to complete goals we constantly evaluate our progress and on personally salient problems (Mason et al., 2013). Thus, much of our internal time is spent judging ourselves and others and worrying about the future (Morin, Uttl, & Hamper, 2011). In this line of thinking spontaneous thoughts generated by the DMN are a double-edged sword. They are adaptive when they serve the optimization of goal pursuit and planning, however they come at an emotional cost.

The hypothesis also makes intuitive sense of common clichés about the benefits of living in the moment as well as eastern philosophical traditions that emphasize the connection between mindfulness, well-being and ultimately egolessness (Millière et al., 2018). It provides a neat explanation both of why depression is associated with rumination, and why meditation relieves depression and increases well-being - simply by reducing harmful self-referential mindwandering and activity in the DMN. However, if this account is to be interpreted narrowly, it is directly contradicted by psychological interventions that increase well-being through positive

thinking. One clear example is the cultivation of gratitude, a practice which revolves around actively bringing up past memories and immersing oneself in the emotions they awaken. Nevertheless, cultivating gratitude has been shown to induce lasting increases in well-being (Emmons & McCullough, 2003; Seligman, Steen, Park, & Peterson, 2005). Similarly, the narrative self is not harmful to mental health, evidenced by how higher coherence of the life story is correlated with increased well-being (Baerger & McAdams, 1999).

In addition, the results from Killingsworth and Gilbert (2010) failed to replicate in two subsequent studies which due to closer intervals between measuring mood and mind-wandering are in a better position to draw conclusions about their order of appearance (Poerio et al., 2013; Song & Wang, 2012). There are also several alternate explanations that have not been sufficiently excluded and the connection between unhappiness and mind-wandering might be attributable to either a third, common cause (Mason et al., 2013). It appears that rather mind-wandering in and of itself being harmful all of the time, its effect on well-being is more dependent on its phenomenological content (Andrews-Hanna et al., 2013).

The replications of the Killingsworth and Gilbert (2010) study suggested that instead mind-wandering arose in response to previous negative affect (Poerio et al., 2013; Song & Wang, 2012). This is corroborated by a study by Smallwood et al. (2009) which shows that inducing a negative mood in participants will lead their minds to wander. This likely reflects the DMN actively inducing mind-wandering as a form of autobiographical problem-solving (Jones, Fournier, & Stone, 2017).

That does however not mean that mind-wandering is wholly benevolent. Though mind-wandering arises in response to personal challenges it might unintentionally serve to maintain the negative mood (Stawarczyk, Majerus, & D'Argembeau, 2013). This could occur either through

reactivation of the negative affect associated with these thoughts (Kross, Ayduk, & Mischel, 2005) or a more indirect effect where mind-wandering increase later access to negatively valenced cognition (Marchetti et al., 2012a). A similar process occurs in insomnia, where rumination and negative thoughts maintain somatic arousal (Mitchell, Mogg, & Bradley, 2012).

In contrast to the hypothesised direction of cause, being self-referential processes lowering mood, it seems as this relationship is bidirectional. However, the fact that there is a bidirectional causal effect between mind-wandering and negative affect allows for the formation of a positive feedback loop. In most people these effects do not take place but in the absence of effective strategies for mental regulation this can escalate into full blown depressive rumination, taking a severe toll on well-being and ability to function.

Rumination acts as a predictor of depression both in remitted individuals and those without previous episodes (Nolen-Hoeksema, 2000). It consists of a repetitive focus on personal problems with a negative focus and self-critical tone (Lyubomirsky, Tucker, Caldwell, & Berg, 1999). It is associated with deficits in attention (Marchetti et al., 2012b), a stronger reaction to negative stimuli and a difficulty disengaging from this negative content (Sheline et al., 2009). This is reflected in the DMN, which displays persistent activity over task positive areas (Marchetti et al., 2012b) and integration with the subgenual ACC during rest is associated with negative rumination (Greicius et al., 2007). In accordance with the association of depression and with narrative self-referential processes it is associated with higher DMN activity (Marchetti et al., 2012b) and increased self-focus (Nolen-Hoeksema, 2000).

Meditation on the other hand is associated with task positive areas and processes that are associated with experiential selfhood (Farb et al., 2007). Meditation activates lateral areas of the CEN that correspond to being "on task". This areas are important in emotional regulation

(Northoff et al., 2011) and their activity is anticorrelated with their DMN (Fox et al., 2005). It is also associated with an increase in bodily awareness and the areas that are associated with it (Lazar et al., 2005) and when these areas are dissociated from the vmPFC it is believed that the bodily states that underlie emotion are interpreted through their objective somatosensory content of the dlPFC rather than their personal affective significance in the vmPFC (Farb et al., 2007). Meditation is also effective as a therapy against depression (Goyal et al., 2014). Meditation increases well-being and decreases rumination (Jain et al., 2007). Consistent with the role of rumination in the recurrence of depression (Kuehner & Weber, 1999) mediation is effective in preventing recurrence (Piet & Hougaard, 2011).

An interesting convergence with a separate line of research is with the use of psychedelic drugs. Both meditation and psychedelics are being investigated as treatments for depression, and interestingly both appear to achieve their effect through attenuation of the DMN and self-related processing (Carhart-Harris et al., 2012; Carhart-Harris et al., 2016; Palhano-Fontes et al., 2015; Ramel et al., 2004). A remarkable example of this is that the long-term antidepressant effect psychedelics is correlated with the degree of ego-dissolution during the psychedelic experience (Roseman, Nutt, & Carhart-Harris, 2018).

How does the paper answer the research question? Is the sense of self a threat to well-being? The DMN is implicated in narrative self-referential processes (Farb et al., 2007) as well as mind-wandering (Raichle et al., 2001). The relationship between these processes and well-being in healthy subjects appears to be more complex than the initial hypothesis. It appears that the causal relationship between them goes both directions and that several factors can complicate the drawing of causal inferences (Mason et al., 2013). Furthermore, DMN activity can confer

several benefits related to planning and problem-solving (Andrews-Hanna, 2012; Baird et al., 2012).

However, depression can be construed as an excess of narrative self-reference and a deficit in experiential self-reference and this is reflected in the brain. The hypothesis that this behaviour roughly mirrors meditation is also taken to be verified. Depression being associated with high levels of spontaneous cognition (Hamilton et al., 2011) and deficient focused cognition (Belleau et al., 2014) increased focus on the self-concept in time (Nolen-Hoeksema, 2000). This is reflected in the brain with a persistently active DMN and hypoactive CEN (Belleau et al., 2014). Meditation on the other hand is associated with decreases both mind-wandering and DMN activity (Brewer et al., 2011), increases in task positive areas (Farb et al., 2007) and increased bodily awareness (Hölzel et al., 2011), corresponding to the experiential self.

The narrative-self is therefore arguably not a threat to well-being. However, if the stream of consciousness becomes stuck in a dark place focusing on the here and now, the breath, and the body is likely to break the cycle.

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