Degree project

Attending to the Now: A Systematic Review of the Neural Correlates of Trait Mindfulness

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Abstract

Trait mindfulness refers to the tendency of being mindful in everyday life. Individuals characterized with high trait mindfulness have reported high subjective wellbeing and are less prone to depression and stress. The aim with this systematic review was to investigate the neural correlates of trait mindfulness. Also, to compare the neural correlates underlying trait mindfulness with those related to mindfulness practices. A systematic search, screening and selection was conducted, resulting in twelve articles included for data extraction and discussion. All studies investigated resting state brain activity or brain structure, measured by fMRI or MRI, in relation to individual scores in trait mindfulness measures. Trait mindfulness was characterized by reduced connectivity within the DMN (between the PCC, the medial PFC, the STG and the thalamus e.g.) and increased functional connectivity between the insula and the ACC within the SN. Further, decreased functional connectivity between the DMN and the SN was observed. No consistent structural correlates characterizing trait mindfulness were reported. Reduced connectivity within the DMN is thought to associate with reduced vulnerability to rumination and depression. Increased connectivity within the SN has been linked to enhanced body awareness and interoception. Decreased functional connectivity between the DMN and the SN has been suggested to facilitate enhanced attention. Trait mindfulness appears to share some neural characteristics with those linked to mindfulness practices: weaker functional connectivity within the DMN, increased involvement of the insula and the ACC within the SN, and weaker connectivity between the DMN and the SN.

Keywords: trait mindfulness, fMRI, MRI, wellbeing

Attending to the Now: A Systematic Review of the Neural Correlates of Trait Mindfulness

Mindfulness is nowadays a familiar term within Western societies. Several practices with the aim to foster mindfulness have been developed (Parkinson et al., 2019). Such mindfulness practices have been shown to provide beneficial effects for physical health and well-being, stress-reduction (Brown et al., 2007; Gotink et al., 2016), emotion-regulation (Brown et al., 2007; Farb et al., 2012), self-esteem (Bajaj et al., 2016), and lead to a decrease in anxiety and depressive symptoms (Chiesa et al., 2015). While *state mindfulness* refers to the momentary state of mindfulness, *trait* (or *dispositional*) *mindfulness* is the tendency to be more mindful in everyday life. In other words, individuals high in trait mindfulness tend to experience mindful states more frequently (Brown & Ryan, 2006; Thompson & Waltz, 2007). While there has been significant research on the neural basis of mindfulness practices and state mindfulness (Young et al., 2018), less is known about the neural basis of trait mindfulness.

The meaning of mindfulness varies depending on context, and no one common definition exists. There are classical Buddhist understandings of mindfulness, with origin in Buddhist philosophical traditions. Within psychological science, multiple scientific definitions of mindfulness have also been proposed (Quaglia et al., 2015). Brown and Ryan (2006) have stated that mindfulness is "open or receptive attention to and awareness of ongoing events and experience" (p. 245). Here, focus lies on attention and awareness, which are receptive features of mindfulness. Kabat-Zinn has additionally brought attention to the attitudinal aspect of nonjudgement. According to him, mindfulness is "paying attention in a particular way: on purpose, in the present moment, and nonjudgmentally" (Kabat-Zinn, 1994, p. 4). Like Kabat-Zinn, Bishop et al. (2006) have noted both receptive and attitudinal features of mindfulness, describing it as "[a] kind of nonelaborative, non-judgmental, present-centred awareness in which each thought, feeling, or sensation that arises in the attentional field is acknowledged and accepted as it is" (p. 232). Although these definitions emphasize slightly different aspects of mindfulness, orientation towards the present experience is common to all of them.

Individual differences in trait mindfulness are best identified among meditation naïve individuals, since experienced meditators, presumably due to practice, score significantly higher in trait mindfulness (Brown & Ryan, 2003). Individuals characterized by high trait mindfulness have especially been shown to feature enhanced *awareness*, i.e. the observation of internal and external environments, and *attention*, i.e. the conscious focus on observed stimuli (Brown & Ryan, 2003).

Due to the various conceptualizations of mindfulness, several measures of trait mindfulness have been developed. Currently, eight self-report scales on trait mindfulness are primarily used (Quaglia et al., 2015). The most common ones are the Mindful Attention Awareness Scale (MAAS; Brown & Ryan, 2003) and the Five Facet Mindfulness Questionnaire (FFMQ; Baer et al., 2006).

The Mindful Attention Awareness Scale (MAAS; Brown & Ryan, 2003) is a 15-item scale that measures individual skills of attention and awareness in everyday life. On a 6-point Likert-type scale, participants are required to rate their frequency of being in an attentive and aware state of mind, from *almost always* to *almost never* (Brown & Ryan, 2003).

Like MAAS, the Five Facet Mindfulness Questionnaire (FFMQ; Baer et al., 2006) measures individual´s everyday mindfulness. This 39-item scale is based on components from several mindfulness measurements, including MAAS. Aspects covered in FFMQ are observing, describing, acting with awareness, nonjudging of inner experience and nonreactivity to inner experience. Participants are required to rate statements on a Likert-type scale, from *never or very rarely true* to *very often or always true* (Baer et al., 2008).

The Freiburg Mindfulness Inventory (FMI; Walach et al., 2006) is another questionnaire that is used to measure trait mindfulness. Here, 14 items of both receptive, "I am open to the experience of the present moment" (Walach et al., 2006, p. 1549), and attitudinal, "I see my mistakes and difficulties without judging them" (Walach et al., 2006, p. 1549), aspects are rated from 1 (*rarely*) to 4 (*always*) (Walach et al., 2006).

Additionally, an objective measure of trait mindfulness, Breath Counting Task (BCT; Wong et al., 2018), are occasionally applied in combination with a subjective self-report (Lim et al., 2018). The BCT measures sustained attention, by asking individuals to count their breath for 20 minutes while their breath rate is objectively registered by a recording device. Participants are instructed to attend the feeling of breathing and quietly count their inhalations in the head from 1 to 9, and to report the counting by pressing one button for 8 breaths and one button for the 9th breath. Then to start over again. The subjective breath count is further compared with recorded breathing rate, in order to determine an individual´s breath counting accuracy (Wong et al., 2018).

There are many different types of mindfulness practices (e.g., Mindfulness Based Stress Reduction (MBSR) and Mindfulness Based Cognitive Therapy (MBCT)) (Kabat-Zinn, 2013). Although different types of practices are associated with different neural networks, some brain regions seem to be involved across different mindfulness practices. According to a relatively recent meta-analysis of functional neuroimaging studies involving both mindfulness experts (long term meditators) and meditation-naïve participants consistent

activation of insula has been shown (Fox et al., 2016). Insula is involved in interoception and is thought to be associated with meditation due to awareness of interoceptive bodily states, such as breath and heartrate, which is encouraged in many practices (Fox et al., 2016). Insula has also consistently showed increased grey-matter volume as a result of meditation. Based on a comprehensive meta-analysis of structural studies on brief meditation practice, increased insular volume has similarly been suggested to specifically relate to practices involving body-awareness (Fox et al., 2014). Some other areas that have consistently shown increased activity across different mindfulness practices are anterior cingulate cortex (ACC) (Fox et al., 2016; Falcone & Jerram, 2018), pre/supplementary motor cortices, and the frontopolar cortex (Fox et al., 2016). The activation of the ACC is supported by increased volume of the ACC as a result of meditation (Fox et al., 2014), and has been proposed to facilitate regulation of emotion and attention. Pre/supplementary motor cortices have been suggested to be involved in regulation of attention and task-relevant actions during meditation. The frontopolar cortex has further been speculated to support the switching of attention between external and internal stimuli, although no clear answer to the function of this region in meditation has been concluded (Fox et al., 2016). Moreover, diffusion tensor imaging (DTI) studies have observed increased density of white-matter structures as a result of meditation, in the corpus callosum e.g. Increased density in this structure has been interpreted to support the previously mentioned alterations in prefrontal areas, as the corpus callosum connects bilateral prefrontal grey-matter structures (Fox et al., 2014). Conversely, meditation has typically involved decreased activity in the posterior inferior parietal lobule and the posterior cingulate cortex (PCC). These findings have further corresponded with structural findings of reduced volume in the temporoparietal junction and the PCC as a result of meditation (Fox et al., 2014). As components of the default mode network (DMN), which is associated with spontaneous thoughts and mind-wandering, reduced activity in these areas has been interpreted as a reduced tendency to mind wander among meditators (Fox et al., 2016; Fox et al., 2014). It is of interest to look at functional networks, such as the DMN, the salience network (SN), the dorsal attention network (DAN), and the central executive network (CEN), as meditation has been shown to affect the connectivity within these networks (Yang et al., 2019). In addition to the structural brain areas mentioned, meditation has also mediated increased volume of the hippocampus, which has been suggested to facilitate reduced stress by the idea of hippocampus supporting learning of appropriate emotional responses (Fox et al., 2014).

Taken together, functional and structural neuroimaging studies converge on brain areas that are linked to meditation (Fox et al., 2016; Falcone & Jerram, 2018; Fox et al., 2014). These neural correlates of state mindfulness have been suggested to explain beneficial

effects of mindfulness practices, such as decreased rumination and anxiety, and increased emotion regulation (Simon & Engström, 2015; Sharp et al., 2018; Zeidan et al., 2014).

Similar to state mindfulness, trait mindfulness has been shown to be related to enhanced well-being. Individuals high in trait mindfulness have higher levels of positive affect, life satisfaction, self-esteem, enhanced emotion-regulation and enhanced resilience toward stressful experiences, and lower levels of negative affect, rumination, perceived stress, emotional distress, depression and anxiety (for a review, see Tomlinson et al., 2018). These associations may be explained by neural mechanisms involved in processes such as stress reduction (Taren et al., 2013), emotion regulation (Creswell et al., 2007), and hedonic and eudaimonic well-being (Kong et al., 2016). Studies on the neural correlates of trait mindfulness have contributed with improved understanding of its relation to many of these beneficial aspects, however, no systematic reviews on the topic have been published.

The aim of this thesis is to conduct a systematic review on the neural correlates of trait mindfulness. This will be done with focus on studies using structural MRI and functional resting state fMRI, and that include meditation naïve participants. The reason for not including task-related studies is due to the difficulty of differentiating neural activity of a certain task from neural activity of trait mindfulness as such. The focus on meditation naïve participants is due to the fact that meditation itself may be associated with structural and functional alterations, which would be difficult to distinguish from trait mindfulness. To fulfil the aim, this thesis will investigate the following research questions: What neural correlates characterize individuals high in trait mindfulness, as compared to those with low trait mindfulness? Do the neural correlates underlying trait mindfulness involve the same brain areas as mindfulness practices? This may help understand the underlying mechanisms of the beneficial effects of high trait mindfulness.

Methods

Literature Search

A literature search in the databases Web of Science, Scopus and PubMed was conducted on the 10th of February 2021. The following keyword combination was used in Scopus and PubMed: (“dispositional mindfulness” OR “trait mindfulness”) AND ((fMRI OR “functional magnetic resonance imaging”) OR (ERP OR “event related potential”) OR (EEG OR “electroencephalography”) OR (MEG OR “magnetoencephalography”) OR (NIRS OR “near infrared spectroscopy”) OR (DTI OR “diffusion tensor imaging”) OR (PET OR “positron emission tomography”) OR “neural correlates” OR “functional connectivity”). In Web of Science the following two search strings were combined: 1) (“dispositional mindfulness” OR “trait mindfulness”), and 2) ((fMRI OR “functional magnetic resonance imaging”) OR (ERP

OR “event related potential”) OR (EEG OR “electroencephalography”) OR (MEG OR “magnetoencephalography”) OR (NIRS OR “near infrared spectroscopy”) OR (DTI OR “diffusion tensor imaging”) OR (PET OR “positron emission tomography”) OR “neural correlates” OR “functional connectivity”).

The search was not limited to any time periods. When possible (i.e., in the databases Web of Science and Scopus), the search was limited to the subject area “neuroscience” and document type “article”.

Inclusion and Exclusion Criteria

The inclusion criteria were 1) Empirical studies that have been peer-reviewed, 2) Only studies that investigate trait mindfulness, 3) Only studies that include objective neuroimaging methods, 4) Only healthy participants, 5) Only adult participants, 6) Only studies published in English, 7) Only meditation naïve participants. The exclusion criteria were 1) Reviews or meta-analyses, 2) Studies including clinical populations only, 3) Studies involving various mindfulness-based practices, 4) Participants with long-term mediation experience.

The reason to merely include studies on a non-clinical adult population was due to the aim of finding out the neural correlates of trait mindfulness. Since individuals with various clinical diagnoses may have alterations in their brain structure or function, including such individuals would not enable understanding of correlates of trait mindfulness as such.

Data Extraction and Synthesis

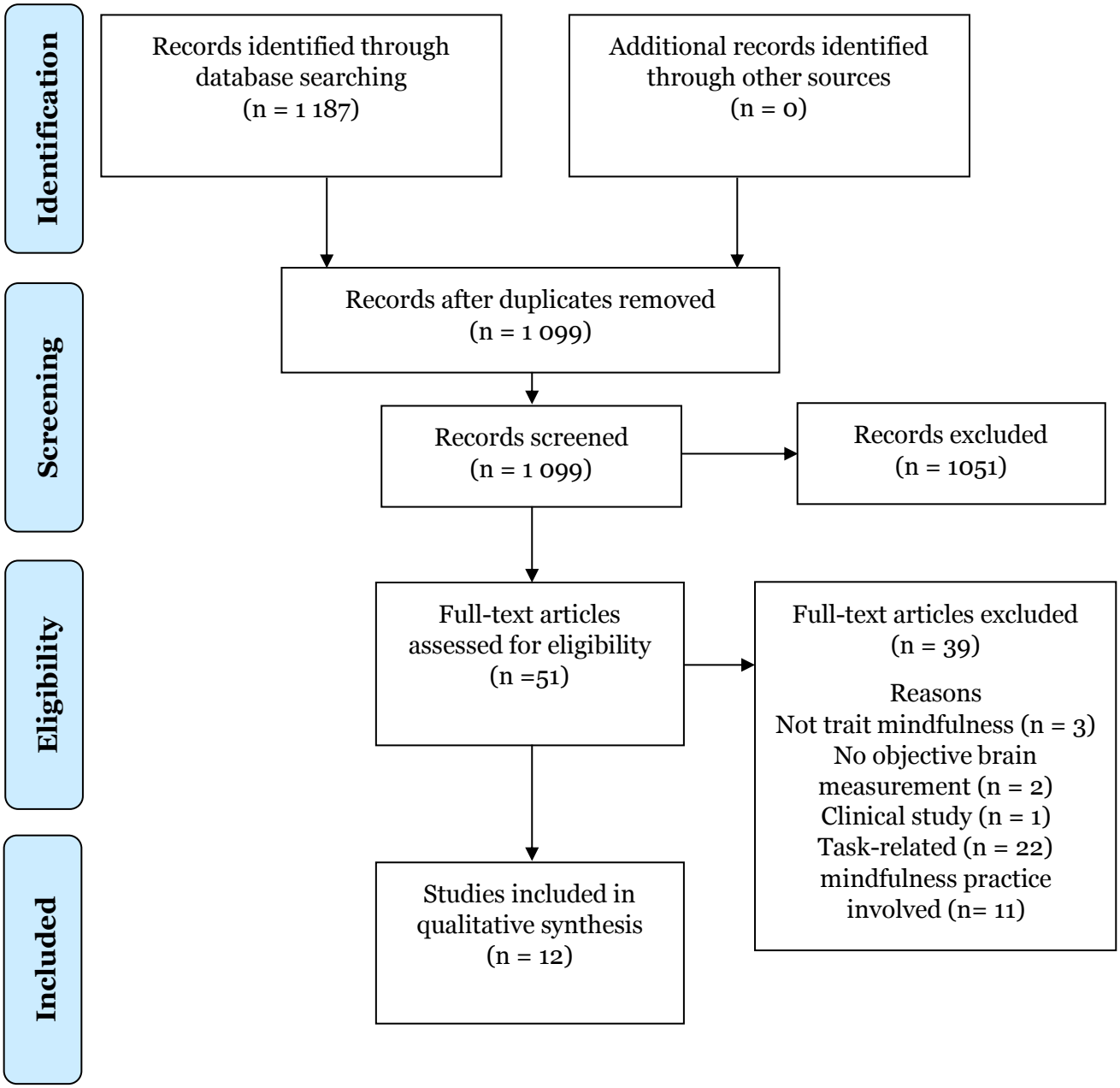
First, database searches using described keyword combinations were conducted by the author. 1 187 articles were found (see PRISMA flow diagram, Figure 1), which were then imported into Rayyan web-based application, a useful tool for management of articles (Ouzzani et al., 2016). First, duplicates were removed, leaving 1 099 articles. Then, the author and a second reviewer (supervisor) independently screened the titles and abstracts of the articles based on the inclusion and exclusion criteria. This procedure was performed using the “blind mode” in Rayyan, which prevents the two reviewers from seeing each other’s decisions. Of the 1 099 articles, the reviewers agreed on including 33 articles but disagreed on 18 articles, resulting in an inter-rater agreement of 98,4 %. The conflicting articles were included into the second screening phase based on full text.

After having conducted the first screening phase, it was clear that several articles meeting the inclusion criteria investigated the neural correlates of trait mindfulness during resting state, while other studies investigated the neural correlates of trait mindfulness while participants were carrying out different tasks. Since the task-based studies included a variety

of different tasks, it was unclear whether a comparison between these would yield any clear answers to the research questions of the present review. As such, a decision was made to focus on resting-state studies only. The second screening phase was conducted with this in mind.

Thus, remaining articles were screened based on the full text. Studies were only included if they investigated structural and functional correlates of trait mindfulness in the resting state (with no concurrent task). Articles that met this and the other inclusion criteria (see above) were included, resulting in twelve articles.

Figure 1
PRISMA 2009 Flow Diagram



Note. PRISMA 2009 Flow Diagram: standard flow diagram used to document the literature search process. Citation: Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. PLoS Med 6(7): e1000097. doi:10.1371/journal.pmed1000097

Results

Methodology of Included Articles

Table 1 presents descriptive information regarding the participants, measurements and study designs included in each study. The total number of participants was 1 362, of which 55% were females. In one study mean age was not presented (Way et al., 2010). Based on remaining studies, mean age ranged from 18-66. All studies included healthy participants only.

Eight studies used MAAS to measure trait mindfulness (Bilevicius et al., 2018; Boekel & Hsieh, 2018; Kong et al., 2016; Lu et al., 2014; Sharuya Prakash et al., 2013; Taren et al., 2013; Wang et al., 2014; Way et al., 2010). One study used FFMQ (Parkinson et al., 2019), one study MAAS and FMI (Doll et al., 2015), one study FFMQ and BCT (Lim et al., 2018), and one study MAAS and FFMQ (Zhuang et al., 2017) to measure trait mindfulness.

Eight studies used functional neuroimaging methods. Of those, five studies used fMRI and whole-brain (WB) analysis (Bilevicius et al., 2018; Doll et al., 2015; Kong et al., 2016; Parkinson et al., 2019; Way et al., 2010). One study used fMRI and region of interest (ROI) analysis of the PCC (Wang et al., 2014). One study used fMRI and ROI analysis of the DMN (Sharuya Prakash et al., 2013). One study used fMRI and ROI analysis of the DMN, the SN, the dorsal attentional network (DAN), and the central executive network (CEN) (Lim et al., 2018). Four studies involved structural neuroimaging methods. Of those three studies used MRI (Lu et al., 2014; Taren et al., 2013; Zhuang et al., 2017) and one study DTI (Boekel & Hsieh, 2018).

The majority of the fMRI studies provided clear instructions for the participants while undergoing the scan. Five of these asked participants to remain relaxed and still with eyes closed, not to think of anything in particular and not to fall asleep (Doll et al., 2015; Kong et al., 2016; Bilevicius et al., 2018; Parkinson et al., 2019; Wang et al., 2014). Two studies asked participants to focus their eyes on a fixation cross, not to think of anything and not to fall asleep (Way et al., 2010; Sharuya Prakash et al., 2013). One article did not describe any instructions given to the participants (Lim et al., 2018).

All studies used a between-subject design. Lim et al. (2018) separated the participants into a high trait mindfulness group (HTM) and a low trait mindfulness group (LTM) based on BCT and FFMQ scores.

Table 1
Characteristics of Included Studies

Article	Participants	Mean age (SD)	Trait mindfulness scale	Neuroimaging method	Study design
Bilevicius et al., 2018	N=32 (22 females)	18.16 (1.08)	MAAS	fMRI WB	Between-subject
Boekel & Hsieh, 2018	N=97 (48 females)	57.26	MAAS	DTI WB	Between-subject
Doll et al., 2015	N=26 (16 females)	26.9 (4.6)	MAAS, FMI	fMRI	Between-subject
Kong et al., 2016	N=290 (157 females)	21.56 (1.01)	MAAS	fMRI WB	Between-subject
Lim et al., 2018	Group 1 HTM: n=21 (13 females) Group 2 LTM: n=18 (13 females)	Group 1: 23.7 (3.4) Group 2: 21.9 (2.3)	FFMQ, BCT	fMRI ROI	Between-subject
Lu et al., 2014	N= 247 (131 females)	21.7 (1.0)	MAAS	MRI	Between-subject
Parkinson et al., 2019	N= 29 (15 females)	19.89 (2.74)	FFMQ	fMRI WB	Between-subject
Sharuya Prakash et al., 2013	N= 25 (19 female)	65.88	MAAS	fMRI WB, ROI	Between-subject
Taren et al., 2013	N=155 (77 females)	40.7 (6.16)	MAAS	MRI	Between-subject
Wang et al., 2014	N=245 (129 females)	21.7 (1.05)	MAAS	fMRI ROI	Between-subject
Way et al., 2010	N=27 (16 females)	"young adults"	MAAS	fMRI	Between-subject
Zhuang et al., 2017	N= 150 (90 females)	19.68 (2.07)	MAAS, FFMQ	MRI	Between-subject

Note. SD= standard deviation. HTM= high trait mindfulness. LTM= low trait mindfulness. MAAS= Mindful Attention Awareness Scale. FMI= Freiburg Mindfulness Inventory. FFMQ= Five Facet Mindfulness Questionnaire. BCT= Breath Counting Task. MRI= magnetic

resonance imaging. fMRI= functional magnetic resonance imaging. DTI= diffusion tensor imaging. WB= whole brain. ROI= region of interest.

Functional Correlates of Trait Mindfulness

Trait mindfulness, as measured by trait mindfulness measures, is associated with activity in or between different brain regions or networks. Bilevicius et al. (2018) aimed to identify associations between MAAS scores and functional connectivity within resting-state networks: the DMN, the SN and the right and left CEN. Reduced within-network connectivity of the DMN was identified, mediated by reduced connectivity between the left medial frontal gyrus (MFG) and the left superior temporal gyrus (STG). The authors suggested weaker connectivity within the DMN to represent reduced mind-wandering. This was supported by Parkinson et al. (2019) who found FFMQ scores to correlate with decreased activity between the right STG, bilateral medial temporal gyri (MTG) and the left inferior temporal gyrus (ITG). Decreased connectivity between the thalamus and the PCC within the DMN was further reported by Wang et al. (2014), who likewise suggested MAAS scores to correlate with reduced tendency for mind wandering. Similarly, Way et al. (2010) reported MAAS scores to correlate with weaker connectivity of the DMN, mediated by reduced connectivity between the PCC, the medial PFC and bilateral amygdala. Based on these findings, the authors suggested MAAS scores to associate with reduced self-referential processing during rest.

Further, consistent findings of increased activity in, and functional connectivity between, components within the salience network (SN) were reported. Kong et al. (2016) found MAAS scores to correlate with increased activity in the right insula, which was interpreted as enhanced body awareness and interoception, and the left orbitofrontal cortex (OFC), suggested to support emotion processing. Bilevicius et al. (2018) reported MAAS scores to associate with increased functional connectivity between the insula and the ACC, which was also suggested to represent greater attention to bodily sensations.

A few studies looked at functional connectivity between resting state networks. Individuals characterized by high trait mindfulness consistently demonstrated decreased functional connectivity between the DMN and other functional networks. Doll et al. (2015) found decreased connectivity between the posterior ventral DMN (pvDMN) and the insular salience network (insSN). The authors suggested this to reflect a more distinct separation between the DMN and the SN in trait mindfulness, thought to facilitate detection of mind wandering. Similarly, Bilevicius et al. (2018) reported decreased connectivity of the cuneus and the precuneus (components of the DMN) with the SN and the CEN. This was indicated to conform with the findings of Doll et al. (2015). Further, Lim et al. (2018) demonstrated decreased connectivity between the DMN and the SN, and between the DMN and the DAN. The authors suggested more frequent activation of the SN and the DAN, referred to as “task-

ready states", and less frequent involvement of the DMN, referred to as an "idling state", to reflect increased attention and awareness in mindful individuals. In line with Doll et al. (2015) and Bilevicius et al. (2018), the authors suggested greater separation of the networks to facilitate detection of mind-wandering.

There were a few reported findings inconsistent with the general findings described. Different from several studies reporting weaker within-network connectivity of the DMN in more mindful individuals, Lim et al. (2018) observed increased connectivity within the DMN to correlate with trait mindfulness, as measured by FFMQ and BCT. Rather than an increased involvement of the DMN, the authors suggested, as described above, this to reflect a more distinct separation between the DMN and more attentive networks (the SN and the DAN). Further, Sharuya Prakash et al. (2013) reported increased DMN connectivity, mediated by the dorsal PCC and precuneus. The authors suggested this to reflect increased internal mentation in individuals characterized by high trait mindfulness, which is contradicting to suggestions of decreased mind-wandering in more mindful individuals (Bilevicius et al., 2018; Parkinson et al., 2019; Wang et al., 2014). Notably, this was observed in a sample of older individuals (mean age 65.9).

Structural Correlates of Trait Mindfulness

Structural characteristics of trait mindfulness have been investigated by comparing individual scores in trait mindfulness measures with individual brain structure, measured by MRI. Lu et al. (2014) observed increased volume of bilateral ACC to correlate with MAAS scores, which was suggested to reflect enhanced attention in more mindful individuals. This by referring to suggestions of the ACC being involved in executive attention (Van Veen and Carter, 2002). Taren el at. (2013) observed MAAS scores to correlate with decreased grey matter volume in the left caudate and the right amygdala. The authors suggested these findings to reflect reduced stress reactivity in individuals characterized by high trait mindfulness. However, Lu et al. (2014) contrarily found MAAS scores to associate with increased volume of the right amygdala/hippocampus, which was interpreted to reflect enhanced emotion regulation in individuals characterized by high trait mindfulness. Further, Lu et al. (2014) reported decreased grey matter volume in bilateral PCC and the left orbitofrontal cortex (OFC). The implication of decreased volume of the OFC was regarded unclear. However, the alteration in the PCC was suggested to support findings of reduced self-referential processing in more mindful individuals (Way et al. 2010). Inconsistent with this, Zhuang et al. (2017) detected increased grey-matter volume in the right precuneus, which surrounds the PCC, to correlate with MAAS scores. The authors suggested increased volume in this area to reflect greater awareness of the self in more mindful individuals. In the same study, Zhuang et al. (2017) also investigated structural characteristics of trait

mindfulness as measured by FFMQ. Here, the facets of *observing, describing, acting with awareness, nonjudging of inner experience* and *nonreactivity to inner experience*, were investigated separately. The *describing* facet correlated with increased volume of the right dorsolateral PFC, the superior PFC and the inferior parietal lobule. The *nonjudging* facet associated with increased volume of the superior PFC. High scores in these facets were interpreted to reflect enhanced attention control and emotion regulation. Interestingly, MAAS scores and FFMQ scores correlated with alterations in different brain areas.

Using structural DTI, Boekel & Hsieh (2018) investigated the relationship between white matter structures and trait mindfulness in older participants (with mean age 57.3). Observed was a positive correlation between trait mindfulness and white-matter density in the internal and external capsule, and in the corona radiata. The authors interpreted these findings to reflect reduced age-related decline in individuals characterized by high trait mindfulness.

Table 2
Results of Included Studies

Article	Method	Activity ↑	Activity ↓
Bilevicius et al., 2018	fMRI WB	Within-network connectivity: DMN (L parahippocampal gyrus, L caudate, R medial frontal gyrus) SN: (L insula, ACC)	Within-network connectivity: DMN (L medial frontal gyri, L superior temporal gyrus, L insula) Between-network connectivity: DMN - SN, DMN – CEN
Doll et al., 2015	fMRI WB	-	Between-network connectivity: insSN - pvDMN
Kong et al., 2016	fMRI WB	R insula, L parahippocampal gyrus, L OFC	R inferior frontal gyrus
Parkinson et al., 2019	fMRI WB	Within-network connectivity: DMN (R anterior cingulate gyrus, R middle cingulate gyrus, R caudate, R medial frontal gyrus) SN: (R cuneus, L cuneus)	Within-network connectivity: DMN (L middle and inferior temporal gyri, L middle and superior occipital gyri, R middle and superior temporal gyri) CEN (R middle and superior frontal gyri)
Way et al., 2010	fMRI WB	-	Within-network connectivity: DMN (mPFC, PCC, bilateral amygdala)

Sharuya Prakash et al., 2013	fMRI WB, ROI (DMN)	Within-network connectivity: DMN (dorsal PCC, precuneus)	-
Lim et al., 2018	fMRI ROI (DMN, DAN, SN, ECN)	Within-network connectivity: DMN, SN	Between-network connectivity: DMN-SN, DMN-DAN
Wang et al., 2014	fMRI ROI (PCC)	-	Within-network connectivity DMN (thalamus, PCC)

Article	Method	Volume ↑	Volume ↓
Lu et al., 2014	MRI	R amygdala/hippocampus, bilateral ACC	Bilateral PCC, L OFC
Taren et al., 2013	MRI	-	R amygdala, L caudate
Zhuang et al., 2017	MRI	MAAS: R precuneus. FFMQ Describing: R dlPFC, inferior parietal lobule, L superior PFC. FFMQ Nonjudging: Superior PFC	FFMQ Nonreactivity: R superior PFC, middle occipital cortex
Boekel & Hsieh, 2018	DTI	WM volume: Internal and external capsule, corona radiata	-

Note. R= right, L= left, BL= bilateral, PFC= prefrontal cortex, ACC= anterior cingulate cortex, PCC= posterior cingulate cortex, OFC= orbitofrontal cortex, WM= white matter. DMN= default mode network, pvDMN= posterior-ventral default mode network, SN= salience network, insSN= insular salience network, CEN= central executive network, DAN= dorsal attention network, ↑= increase, ↓= decrease.

Discussion

The aim of this systematic review was to investigate the neural correlates of trait mindfulness. The literature search and screening process resulted in twelve studies included for data extraction and synthesis. Here, findings regarding the functional and structural brain correlates of trait mindfulness will be discussed.

What neural correlates characterize individuals high in trait mindfulness, as compared to those with low trait mindfulness?

Studies using functional and structural neuroimaging measures identified structures and resting state activity patterns that characterized individuals with high trait mindfulness scores. Most consistently, reduced functional connectivity between components within the DMN was observed in individuals characterized by high trait mindfulness, such as the PCC (Wang et al., 2014; Way et al., 2010), the thalamus (Wang et al., 2014), the medial PFC, the amygdala (Way et al., 2010), the MFG, and the STG (Bilevicius et al., 2018). This supports the idea of mindful individuals engaging less in mind wandering and self-referential thoughts during rest. Further, increased activity in the insula (Kong et al., 2016), as well as increased functional connectivity between the insula and the ACC within the SN, was observed (Bilevicius et al., 2018; Lim et al.,2018). Individuals characterized with high trait mindfulness moreover demonstrated reduced functional connectivity between the DMN and other functional networks: the SN and the DAN (Doll et al., 2015; Lim et al., 2018). Some structural findings supported functional findings characterizing trait mindfulness, such as increased ACC volume and decreased PCC volume (Lu et al., 2014). Although, findings on structural characteristics of trait mindfulness were few and inconsistent. The implications of the functional and structural findings will be discussed below.

The DMN is often associated with self-referential processing (Andrews-Hanna et al., 2010) and mind wandering (Buckner et al., 2008). In contrast to mindfulness, which has been defined as attention to and awareness of ongoing events, mind wandering refers to fluid shifting between thoughts and events in the environment (Brown & Ryan, 2006). Accordingly, as demonstrated in more mindful individuals, reduced functional connectivity within the DMN has been interpreted as reduced tendency to engage in self-referential processing and mind wandering. Self-referential rumination is linked to enhanced risk for depression (Nolen-Hoeksema, 2000) and has further been associated with increased activity in the medial PFC (Ray et al., 2005). Accordingly, Way et al. (2010) have argued that reduced activity in self-referential processing areas may underlie less vulnerability for rumination and depression in individuals characterized by high trait mindfulness. The authors speculated that this neural characteristic may lead more mindful individuals to be less attached to thoughts and feelings associated with the self. This idea of detachment from the self is further related to a core technique in MBCT, which encourages metacognitive awareness of negative self-referential thoughts. Notably, MBCT has successfully targeted depressive symptomatology (Kuyken, et al., 2008). Wang et al. (2014) further specifically suggested observed reduced connectivity between the thalamus and the PCC to account for reduced self-referential processing. This by referring to evidence of the thalamus being a generator of the alpha rhythm (8-12 Hz) (Hughes & Crunelli, 2005), which has been associated with mind wandering and self-referential processing (Ros et al., 2013). Interestingly, in contrast to the general observation of decreased functional connectivity within the DMN, Sharuya Prakash

et al. (2013) reported increased DMN connectivity, mediated by the dorsal PCC and the precuneus. The authors suggested this to reflect increased internal mentation in older individuals characterized by high trait mindfulness. This contradicting idea may be viewed as an exception to the dominant suggestion of reduced DMN connectivity, interpreted as less mind wandering and self-referential processing in more mindful individuals.

Further, individuals who score high in trait mindfulness measures have been characterized with greater activity in, and functional connectivity between, components within the SN. The SN is involved in the integration of internal and external homeostatic relevant information, interoception (Seeley, 2019). Interoceptive skills, of detecting visceral stimuli, have further been associated with better emotion processing (Critchley & Garfinkel, 2017). Accordingly, a speculation would be that the involvement of the SN in interoception may be associated with reported enhanced emotion regulation skills in individuals characterized with high trait mindfulness (Deng et al., 2020).

Moreover, increased anti-correlation between the DMN and the SN observed in individuals who score high in trait mindfulness measures has been suggested to represent a more distinct separation between the networks. This has been suggested to facilitate enhanced ability to detect mind-wandering (Doll et al., 2015; Bilevicius et al., 2018; Lim et al., 2018). Lim et al. (2018) have further demonstrated how mindful individuals spend more time in a “task-ready state”, referring to activation of the SN and the DAN, as opposed to an “idling state”, referring to activation of the DMN. The authors interpreted this to reflect enhanced attention and awareness in mindful individuals. Moreover, the SN has been proposed to be involved in the switching between the DMN and the CEN activation (Goulden et al., 2014; Sridharan et al., 2008). Based on this, Bilevicius et al. (2018) have suggested the SN to support the switching between a less mindful state to a more mindful state, e.g., from mind-wandering to focused attention. In sum, decreased functional connectivity between the DMN and other functional networks support the idea of individuals with higher trait mindfulness being more attentive and aware of internal and external stimuli, and less engaged in in mind-wandering.

Generally, studies investigating structural characteristics of trait mindfulness have generated mixed findings. Given the few structural studies included, i.e., three MRI studies and one DTI study, it is difficult to draw any general conclusions. However, some structural findings are consistent with findings on functional characteristics of trait mindfulness. Lu et al. (2014) for instance found increased volume of the ACC to associate with MAAS scores, which is in line with reported increased involvement of the ACC. The authors emphasized this finding to support the definition of mindfulness as enhanced attention and awareness (Brown & Ryan 2003), by referring to suggestions of the ACC being involved in executive

attention (Van Veen and Carter, 2002). Lu et al. (2014) further compared observed reduced grey-matter volume of the PCC with reduced PCC connectivity (with the medial PFC and the amygdala) in more mindful individuals, which has been interpreted as a lower tendency to ruminate (Way et al., 2010). Although, Zhuang et al. (2017) contrarily detected MAAS scores to associate with increased grey-matter volume in the right precuneus, which surrounds the PCC, with suggestions of this to reflect greater awareness of the self. Thus, Lu et al. (2014) and Zhuang et al. (2017) reported contradicting alterations in an area that has been linked to self-referential processing, which makes it difficult to draw any fair conclusion. Similarly, contradicting observations of MAAS scores to correlate with increased grey matter volume of the right amygdala (Taren el at., 2013) and decreased volume of the right amygdala/hippocampus (Lu et al., 2014) reflect inconsistent findings.

In short, trait mindfulness appears to be characterized by reduced connectivity of self-referential processing areas, which is thought to underlie reduced vulnerability to rumination and depression in individuals characterized by high trait mindfulness. Further, these individuals demonstrate increased involvement of the SN, which link to enhanced body awareness and interoception. Moreover, decreased functional connectivity between the DMN and the SN has characterized trait mindfulness, suggested to facilitate enhanced attention. There are no clear conclusions regarding structural characteristics of trait mindfulness.

Do the neural correlates underlying trait mindfulness involve the same brain areas as mindfulness practices?

Reduced functional connectivity between self-referential processing areas within the DMN, demonstrated in individuals characterized by high trait mindfulness, is comparable with similar neural characteristics as a result of meditation practice (Fox et al., 2016). Further, functional and structural alterations in the insular cortex in particular, and the ACC to some extent, as a result of short-term meditation in meditation naïve participants (Falcone & Jerram, 2018; Fox et al., 2016; Fox et al., 2014), may be comparable with reported increased connectivity between the insula and the ACC in individuals characterized by high trait mindfulness. Given the involvement of the SN in interoception, it is further logical that experienced meditators have demonstrated enhanced interoceptive accuracy, compared to non-meditators (Daubenmier et al., 2013). As enhanced interoceptive skills has been linked to better emotion regulation (Price & Hooven, 2018), a speculation would be that involvement of the SN may underlie better emotion regulation reported in both meditators (Brown et al., 2007; Farb et al., 2012) and individuals characterized by high trait mindfulness (Tomlinson et al., 2018). Further, Bilevicius el al. (2018) have compared involvement of the ACC in trait mindfulness to long-term meditation, which has been shown to induce greater theta activity in ACC neurons (Tang et al., 2009), and greater density of white matter

pathways associated with the ACC (Tang et al., 2012). Moreover, similar to reported reduced connectivity between the DMN and the SN in individuals characterized by high trait mindfulness, decreased connectivity between the DMN (the PCC and the vmPFC) and the insular SN has been reported in experienced meditators (Hasenkamp and Barsalou, 2012).

Taken together, the neural correlates underlying trait mindfulness appear to involve several brain areas and characteristics of functional networks that are linked to mindfulness practices.

Limitations of Reviewed Studies and Suggestions for Future Research

Possible limitations in the methodology of the studies included in this systematic review need to be considered. Regarding neuroimaging methods, the studies were generally similar in their procedure and instructions to participants. However, the included studies conducted eihter a WB analysis or a ROI analysis (or both). As ROI analyses target a specific brain area or network, in accordance with an a priori hypothesis, a chance is that any unexpected findings may go unnoticed. Reversely, WB analyses may result in relevant, but also irrelevant findings. Further, as different methodologies may result in different findings, the transferability might be limited. Further, a major issue is the use of different scales measuring trait mindfulness. As described in the Introduction section, different types of measures focus on slightly different aspects of mindfulness. For instance, while MAAS (Brown & Ryan, 2003) focuses on receptive features of attention and awareness, FFMQ (Baer et al., 2006) and FMI (Walach et al., 2006) cover attitudinal features of acceptance and non-judgment. Zhuang et al. (2017) showed that different measures are associated with different neural correlates. While MAAS scores correlated with altered grey matter volume in precuneus, which was interpreted to reflect greater self-awareness, the facets of FFMQ were associated with areas engaged in attention control and emotion regulation. Doll et al. (2015) further suggested that decreased between-network connectivity of the pvDMN and the insSN specifically related to FMI. Based on this, when comparing studies using different trait mindfulness measures results should be interpreted carefully.

Moreover, the number of participants varied drastically between the studies. While Sharuya Prakash et al. (2013) included 25 participants in their study, Kong et al. (2016) included 290 participants. Since the focus is on between-subject comparison, large sample sizes are needed. Given that 55 % of the participants were female, no gender bias should be expected to have affected the result. Regarding age, the majority of the studies included participants of a younger mean age, while some studies had a relatively high mean age. As neural function and structure vary with age (Boekel & Hsieh, 2018), an overrepresentation of young participants may not account for results of a heterogeneous population. Notably,

Sharuya Prakash et al. (2013), who included participants with a mean age of 65.9, suggested individuals characterized with high trait mindfulness to engage more in mind-wandering. This suggestion contradicted with several studies including a considerably younger population, pointing at a reduced tendency to engage in mind-wandering in more mindful individuals (Bilevicius et al., 2018; Parkinson et al., 2019; Wang et al., 2014).

Given the limitation of using different measures of trait mindfulness, specific aspects of mindfulness as measured by a given scale should be clearly distinguished in future studies. One solution may be to agree on one measure that always should be used when measuring trait mindfulness. That way, findings may be more reliably comparable. Further, a greater variety in age may represent the population better. Moreover, more studies on structural correlates of trait mindfulness should be conducted.

Ethical and Societal Aspects

This systematic review only included studies including healthy adult populations. No study reported exposing participants to any major risks. Therefore, no ethical problems are inherent to the studies. On a societal level, research on neural correlates of trait mindfulness contributes with an objective perspective to subjective and behavioral characteristics of trait mindfulness. This may not only bring a nuanced understanding of the neural mechanisms underlying wellbeing but may also give rise to further understanding of individual differences. Moreover, as experienced meditators score significantly higher in MAAS and FFMQ, as opposed to less experienced or non-meditators, trait mindfulness is presumably alterable by practice (Wheeler el al., 2017). Given the beneficial aspects of high trait mindfulness, some of which have been targeted in the present review, this suggestion may be seen relevant in the light of promoting enhanced subjective wellbeing.

Conclusion

The aim of this thesis was to conduct a systematic review on the neural correlates of trait mindfulness. The main functional neural characteristics of trait mindfulness included reduced connectivity between self-referential processing areas within the DMN, such as the PCC, the medial PFC, the STG and the thalamus, which is thought to associate with reduced vulnerability to rumination and depression. Further, increased functional connectivity between the insula and the ACC within the SN was identified in individuals characterized by high trait mindfulness. This characteristic has been linked to enhanced body awareness and interoception. Moreover, decreased functional connectivity between the DMN and the SN was observed, suggested to facilitate enhanced attention. No consistent structural correlates characterizing trait mindfulness were reported. With regard to the second research question, trait mindfulness appears to share some neural characteristics with those linked to

mindfulness practices: weaker functional connectivity within the DMN, increased involvement of the insula and the ACC within the SN, and weaker connectivity between the DMN and the SN. Incoherent use of trait mindfulness measures limits the comparison of the results, future studies should apply a more consistent methodology. Also, more studies on structural characteristics of trait mindfulness should be conducted. This may facilitate more reliable conclusions on neural correlates of trait mindfulness, hence reveal underlying mechanisms of beneficial effects of high trait mindfulness related to wellbeing.

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