# Toward a Brain Network Science of Mindfulness

Isaac N. Treves[a,b,c], Clemens C.C. Bauer[b,d], Matthew D. Sacchet[e], Keara D. Greene[d], Aviva Berkovich-Ohana[g,h,I,j], Susan Whitfield-Gabrieli [b,d,f]

[a]Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, 43 Vassar Street, Cambridge, Massachusetts, 02139, United States of America

[b]McGovern Institute for Brain Research, Massachusetts Institute of Technology, 43 Vassar Street, Cambridge, Massachusetts, 02139, United States of America

[c]Hock E. Tan and K. Lisa Yang Center for Autism Research, Massachusetts Institute of Technology, 43 Vassar Street, Cambridge, Massachusetts, 02139, United States of America

[d]Department of Psychology, Northeastern University, 805 Columbus Ave, Boston, MA 02120 USA

[e]Meditation Research Program, Department of Psychiatry, Massachusetts General Hospital, Harvard Medical School, Boston, MA, USA

[f]Department of Psychiatry, Massachusetts General Hospital, Harvard Medical School, Boston, MA, USA

[g]Edmond Safra Brain Research Center, Faculty of Education, University of Haifa, Israel

[h]The Integrated Brain and Behavior Research Center (IBBRC), University of Haifa, Israel

[i]Faculty of Education, Department of Learning and Instructional Sciences, University of Haifa, Israel

[j]Faculty of Education, Department of Counseling and Human Development, University of Haifa, Israel

## Author Note

Correspondence regarding this chapter should be directed to Isaac Treves at treves@mit.edu, Building 46-4037, Massachusetts Institute of Technology, 43 Vassar Street, Cambridge, Massachusetts, 02139, United States of America

## Abstract

Resting-state functional magnetic resonance imaging (fMRI) provides a new window into the brain bases of mindfulness. In resting-state scans, participants lie in the scanner in a state of wakeful rest, and low-frequency fluctuations of the brain signals are measured. These brain fluctuations cohere into networks like the default-mode network (DMN), the salience network (SN), and the central executive network (CEN), each with different functional roles and different topography. In this chapter, we summarize and synthesize the literature on resting-state functional connectivity (FC) and mindfulness. We provide a mechanistic model of how networks like the DMN, SN, and CEN interact to produce a state of mindfulness, and the role of mindfulness expertise. We review how resting-state FC may change with mindfulness interventions, and how trait mindfulness might relate to trait-like variation in resting-state FC. Broadly, the extant literature provides several network signatures of mindfulness, including: reduced within-DMN connectivity, anticorrelations between the DMN and attentional networks, increased dynamic flexibility, and more. We additionally discuss discrepancies in the mindfulness FC literature and suggestions toward addressing them. Finally, we describe future directions including network-based fMRI neurofeedback during mindfulness skill acquisition.

*Keywords:* mindfulness, meditation, fMRI, Resting-state, functional connectivity, DMN

## Toward a Brain Network Science of Mindfulness

Systematic inquiry into meditation has existed for millennia. Buddhist traditions in particular have established texts (e.g., the Abidharma) that explore the nature of meditation and the insights it gives into the mind. For the novice practitioner, this knowledge, built upon the experiences of many individuals before them, is a powerful aid in cultivating positive qualities of mind through practice. Recently, a new source of knowledge has emerged from the biological sciences through a new form of inquiry, brain imaging. Brain imaging operates on the fundamental assumption that the biological brain is the seat of the mind, and thus understanding human biology helps you understand the human mind. Brain imaging is promising because it offers objective measurements of what is happening during meditation and what changes after meditation practice. This may help us share knowledge between individuals that come from different meditative traditions (as well as individuals with no prior experience). Brain imaging may additionally help us understand features of the mind and why it takes repeated practice to change them, e.g. brain plasticity. Lastly, brain imaging can provide new insights into mental health and well-being and why meditation may be beneficial. In this chapter, we hope to shed light on the promise of brain imaging for understanding meditation, with careful consideration of its limitations.

## Brain Imaging: Resting-State fMRI

The idea that the brain is the seat of the mind has a long history (Adelman, 1987). In ancient times, people were divided between the heart and the brain as the seat of thought, sensation, emotion, and cognition (Adelman, 1987; Kandel et al., 2000). Hippocrates argued that the brain was the seat of thought, sensation, emotion, and cognition (Adelman, 1987). Galen, a 2nd-century physician, suggested that the brain's fluid-filled cavities were the seat of complex thought and determined personality (Adelman, 1987; Smith, 1971). However, it was not until the late 17th century that the brain's solid tissue was recognized as the seat of intelligence, memory, and thought (Steno, 1965). Since it was recognized that the brain is the seat of the mind, researchers developed a plethora of tools to investigate its structure and function. Numerous different measurements have been offered to explain the function and dysfunction of the mind/brain, ranging from early phrenology to current state of the art neuroimaging. Before the widespread use of neuroimaging, behavioral neurology (Geschwind, 1974), neuropsychology (Mesulam, 1990), and cognitive science (Rumelhart et al., 1986) were all advancing the notion that the brain is an interconnected network with distributed functional systems (Ramón y Cajal, 1990).

Functional MRI (fMRI) has emerged as the technique of choice for examining systems-level brain function due to its high spatial resolution and noninvasive nature (Chen et al., 2020). The signal measured with fMRI is the blood-oxygen-level-dependent (BOLD) signal (Ogawa et al., 1992). When brain cells become more active, they use more oxygen, which is supplied by blood vessels in the region. The flood of oxygenated blood causes a resulting distortion of the magnetic field in the area. This change can be picked up with a specific type of MRI scan called functional MRI, and the signal is called the BOLD signal. When a participant performs a task or is presented with a stimulus, researchers can detect changes in BOLD signal in specific brain regions. Researchers use this information to understand which brain regions are involved (or 'activated') in specific tasks or experiences. In summary, brain activity is linked to changes in blood flow and oxygen levels, which can be measured using fMRI. These measurements can additionally be used by scientists to understand how different brain regions work together.

In the absence of any stimulus or task, temporal correlations between BOLD signals in different brain regions can be assessed to collect a measure of 'resting-state functional connectivity'. This was pioneered by Biswal et al., (1995) in the study of primary sensorimotor cortex during rest. Biswal et al., (1995) showed a strong temporal connection of spontaneous low-frequency signal fluctuations (SLFs) both within and across hemispheres. After removing the fundamental and harmonic components of respiration and heart rate, brain signals from the sensorimotor area and its adjacent cortices were highly correlated, and only a small percentage of signal timecourses (3%) in locations outside the motor cortices were correlated. The SLFs are what produce this linked signal. In short, signals from sensorimotor areas in different hemispheres were temporally aligned even without any sensorimotor stimulation or behavior, suggesting similar function.

By demonstrating these relationships over wider parts of the sensorimotor cortex (i.e., spanning many slices), Lowe and colleagues (1998) expanded upon the findings of Biswal et al. (1995). These and other subsequent studies (Hampson et al., 2002, 2004; Xiong et al., 1998, 1999) established the foundation for "resting-state functional connectivity studies" (rsFC) using fMRI (Greicius et al., 2004; Gusnard & Raichle, 2001). Bressler (1995) suggested that correlated SLFs may be a phenomenon representing the functional connection of cortical areas analogous to the phenomenon of "effective connectivity," where one neuronal population can influence another neuronal population (Friston et al., 1993). rsFC has become more and more popular over the past few decades as a technique for examining human brain networks (J. Zhang et al., 2021). Brain networks may consist of spatially distributed regions across the brain with similar BOLD signals at rest (assessed by rsFC) and in response to tasks.

## Brain Networks

The triple brain networks have received particular attention. They consist of three large-scale networks in the brain: the default mode network (DMN), the salience network (SN), and the frontoparietal network (FPN), also called the central executive network (CEN) (**Figure 1**). Each of these networks consists of distributed brain regions, which are highly intercorrelated during rest. The DMN is involved in mind-wandering (inattention to stimuli and tasks in the present moment) (Buckner et al., 2008; Christoff et al., 2009), is deactivated during attention-demanding tasks (Fox et al., 2005; Hellyer et al., 2014) and consists of brain areas such as the precuneus, posterior cingulate cortex (PCC), inferior parietal lobule, and ventromedial prefrontal cortex (vMPFC; Raichle et al., 2001). Particularly the cortical midline structures of the brain that are core hubs of the DMN (i.e., PCC and vMPFC) have been found to consistently activate when participants engage in narrative self-processing (Gusnard & Raichle, 2001; Kelley et al., 2002; Northoff et al., 2006; Sajonz et al., 2010). The FPN is involved in externally focused, goal-directed attention, and consists of lateral frontal and parietal areas (Seeley et al., 2007). The SN is involved in stimulus-driven attention (‘salience detection’) and consists of the insula and mid-cingulate (Seeley et al., 2007). One perspective on the SN is that it operates as a ‘switch’ between internally focused attention mediated by the DMN, and externally focused attention mediated by the FPN. Additional networks that overlap in areas with the FPN and SN are the dorsal and ventral attention networks (Corbetta et al., 2008).

## The Roles of Brain Networks During Mindfulness Meditation

As is explicated elsewhere in this book, mindfulness refers to a complex family of attention regulatory strategies and practices with a focus on paying attention to the present moment. One common mindfulness practice is *breath awareness*, which involves orienting attention to one’s breath and practicing returning to the breath every time one’s attention wanders away (Lutz et al., 2008). Networks like the DMN, FPN/CEN, and SN, with their roles in attentional processes, may thus be involved in mindfulness practice. Beyond the attentional roles of the differing networks, they are also involved in different modes of self-processing, e.g., narrative vs. embodied self-processing (Christoff et al., 2011). Indeed, it has been shown that long-term mindfulness practice can alter self-processing, based on alterations in the brain network's activity and connectivity (recently reviewed by Giommi et al., 2023). Here, we adopt the attentional roles of the brain networks, building on a mechanistic model of mindfulness advanced by Hasenkamp et al. (2012). They had participants practice a breath-focused attention task in the scanner and press a button when they noticed that their mind wandered. The authors then examined network activations during different periods of the task. First, they found the CEN is involved in sustaining attention to the object (breathing) held in mind. Then, when the mind wanders away from the object, the DMN may become active. Then, when the SN becomes active, the participant may notice their mind wandering. Lastly, to shift their attention back to the object of practice, the participant engages the CEN again.

In summary, mindfulness may involve a process of shifting, refocusing, and sustaining attention involving the SN and CEN networks, and it may involve suppressing mind-wandering through downregulation of the DMN. As individuals practice mindfulness and engage these brain networks, the networks may show enduring changes. These changes may be present during mindfulness meditation, but also in a wakeful, resting-state condition. To investigate this possibility, researchers have compared resting-state functional connectivity before and after mindfulness interventions. Two recent reviews comprehensively examined changes in rsFC as a result of mindfulness training (meta-analysis, Rahrig et al., 2022; systematic review, Sezer et al., 2022). In this chapter, we summarize these results, as well as converging evidence from the study of trait (dispositional) mindfulness and experienced mindfulness meditators.

## Empirical Studies

### Mindfulness Interventions and Resting-State Functional Connectivity

Intervention studies may involve short, intensive retreats (e.g. Taren et al., 2015), as well as standardized interventions like mindfulness based stress reduction (MBSR: e.g. Kral et al., 2019). We identified 20 studies of mindfulness interventions and resting-state fMRI (**Table 1**). Most studies look at functional connectivity, but some use other methods like amplitude of low-frequency fluctuations (ALFF). The functional connectivity studies generally use seed-based analyses, where one region of interest (ROI) is selected, and then correlations with other areas are assessed to see if they increase or decrease with the intervention. Studies have often used seeds within the triple networks, e.g., PCC in default-mode network, ACC in salience network, and DLPFC in the central executive / frontoparietal network. Connectivity within and across these networks may have implications for self-awareness and attention (Buckner et al., 2008; Corbetta et al., 2008; Seeley et al., 2007). In addition, some studies have examined amygdala - prefrontal/ cingulate cortex connectivity, with implications for emotion regulation and stress (Ochsner & Gross, 2005). Here we describe a couple of the most influential studies. For a full review, see Sezer et al., 2022.

In one large-sample study, 130 adults underwent resting-state scans before and after a 3-day intensive mindfulness meditation retreat compared to a matched 3-day relaxation retreat (Taren et al., 2015). At baseline, connectivity between the subgenual-anterior cingulate cortex (sgACC) and amygdala was positively correlated with stress over the last month. This is in accordance with roles for the amygdala and sgACC individually in stress responses (Arnsten, 2009; Gianaros et al., 2008). The mindfulness retreat decreased sgACC-amygdala connectivity. This suggests a possible pathway for mindfulness-based stress reduction.

As discussed above, the DMN is a network of brain regions that is active when an individual is not engaged in any specific task and is instead focused on internal thoughts and self-reflection. Anticorrelations refer to the negative correlation between the activity of two brain regions. The DMN is widely shown to be anticorrelated with multiple-task-positive areas including the CEN during tasks (Brewer et al., 2011; Hellyer et al., 2014; Martinez-Gutierrez et al., 2022; Wen et al., 2013). A series of studies examined the relationship between the DMN and CEN and how it might change with mindfulness training. In one study, 140 adults were randomized to MBSR, a health-enhancement control intervention, and waitlist (Kral et al., 2019). The adults in the MBSR condition showed increases in DMN (specifically the PCC)-CEN (specifically the DLPFC) connectivity, and those who practiced more showed the strongest increases. This has also been found by King et al. (2016), who showed increased DMN-CEN connectivity in veterans receiving mindfulness-based exposure therapy, and the degree of DMN-CEN connectivity correlated with decreases in PTSD symptoms. Finally, Creswell et al. (2016) found increases in DMN-CEN connectivity after a 3-day intensive mindfulness retreat, and the degree of increase correlated with improvements in a marker of inflammatory disease risk. It would seem that there is a strong case to be made that mindfulness increases DMN-CEN connectivity. However, one study in 40 children found increases in DMN (network seed)-CEN (network seed) ***anticorrelation*** pre-post a mindfulness intervention compared to an active coding control group (Bauer, Rozenkrantz, et al., 2020). This anticorrelation was related to sustained attention performance on a behavioral task. For this reason, and because of results from dynamic functional connectivity (**Box 1**) and trait mindfulness studies (**Table 2**), it may be premature to conclude that mindfulness increases DMN-CEN connectivity.

Another approach to network analysis is independent component analysis, or ICA, which is a data-driven, hypothesis-free computational method that finds spatially and temporally independent brain networks. An ICA-based study looked at auditory and visual networks and how they might change due to a mindfulness intervention (Kilpatrick et al., 2011). Participants were instructed to mindfully pay attention to scanner sounds during fMRI acquisition. The MBSR group showed increased functional connectivity within auditory and visual networks, as well as decreased connectivity between them, compared to controls. The effects in the auditory network may have been due to the instruction to "listen to sounds" during the scan. The study also found increased connectivity between the dmPFC and pgACC in the MBSR group, indicating increased awareness of attentional and sensory experience. Decreased functional connectivity was also observed between a region in the cuneus and a composite network including nodes of the SN, FPN, and auditory network. However, the use of composite networks from ICA makes the interpretation of the results challenging.

As can be observed from these studies, and **Table 1**, findings are often inconsistent. A meta-analysis of mindfulness interventions using voxel-based methods was conducted (Rahrig et al., 2022). The authors identified significantly greater rsFC (MT > control) between the left middle cingulate, located within the SN, and the posterior cingulate cortex, a key hub of the DMN. They also didn’t find any evidence of publication bias, which is important as publication bias has been observed elsewhere in mindfulness studies (e.g., Maglione et al., 2017, for a review see Goldberg et al., 2022). This increase in DMN-SN connectivity can be interpreted as relating to increased flexible control of internal attention. Notably, a systematic review of 7 studies involving task-related fMRI (Young et al., 2018) assessed flexibility in brain functioning associated with 8-week mindfulness interventions, and the most consistent longitudinal effect observed was increased insular cortex activity (Salience network), with less consistent activations in the ACC and DLPFC (Control network).

## Trait Mindfulness and Resting-State Functional Connectivity

Individuals may also vary naturally in their disposition or tendency to be mindful in daily life. Self-report questionnaires are commonly used to investigate this ‘trait’ mindfulness (although see Levinson et al., 2014 for a proposed objective measure). Self-report questionnaires include the Mindful Attention Awareness Scale (MAAS) and the Five-Facet Mindfulness Questionnaire (FFMQ). The MAAS is a single-factor scale that consists of 15 items that measure one’s tendency to make attentional lapses throughout everyday life (it is reverse scored) (Brown & Ryan, 2003). The FFMQ is a 39-item scale that consists of five facets – acting with awareness, nonreactivity, non-judging, observe, and describe (Baer et al., 2006). Each facet is considered an essential element of being mindful. The between-individual variation in these self-report scales can be compared to variation in functional connectivity (**Table 2**).

In one study, 40 healthy volunteers completed the FFMQ and then were imaged while resting in the scanner (Harrison et al., 2019). The researchers looked at the correlations between a seed from the DMN (the precuneus) and other brain regions. Those who were higher in trait mindfulness exhibited less connectivity with the mPFC (another node of the DMN). In another study, 245 healthy adults completed the MAAS and then were imaged (Wang et al., 2014). The researchers first identified nodes of the DMN by constructing a PCC seed and selecting the areas correlated with it. Wang et al. (2014) then examined the network properties of each node of the DMN using graph theory, calculating nodal degree, nodal efficiency, and nodal clustering coefficient. They found that these indices in the thalamus negatively correlated with trait mindfulness. Their interpretation was that the more isolated the thalamus from other nodes of the DMN, the greater the mindfulness score. These studies and others have found trait mindfulness is associated with decreased connectivity within the default mode network (Bilevicius et al., 2018; Doll et al., 2015; Harrison et al., 2019; Wang et al., 2014 but see Hunt et al., 2022; Shaurya

Prakash et al., 2013 for contrasting findings). These findings generally align with LTM and intervention studies, which have found both decreases in connectivity (Bauer et al., 2019; Taylor et al., 2013 c.f., Jang et al., 2011) and decreased activations (Brewer et al., 2011; Garrison et al., 2015) of the DMN. These changes in the DMN may be implicated in diminished mind-wandering in more mindful individuals (Mrazek et al., 2012).

Another common finding in trait mindfulness studies is diminished DMN-SN connectivity. In Doll et al. (2015), the authors examined resting-state scans from 26 healthy adults after a two-week intervention (they didn't collect baseline measures). They identified 7 networks using ICA. They found the degree of decreased correlations (increased anticorrelations) between an insular salience network component (insSN) and a posteroventral DMN component was related to scores on the Freiburg Mindfulness Inventory (Walach et al., 2006). Decreased DMN-SN correlations have been found in other trait studies (Lim et al., 2018; Marusak et al., 2018; Mooneyham et al., 2017), intervention studies (Turpyn et al., 2021; Yang et al., 2019), and cross-sectional meditator studies (Bauer et al., 2019). However, a meta-analysis found mindfulness interventions increased DMN (posterior cingulate) -SN (left middle cingulate) correlations (Rahrig et al., 2022). The discrepancy may have to do with the seeds used, see Discussion.

## Resting-State Functional Connectivity in Expert Meditators

In cross-sectional studies, samples of long-term meditators (typically Vipassana or Zen), are compared to novice samples. In addition, correlations between amount of practice (expertise) and functional connectivity can be assessed. Studies have reported reduced FC in experienced meditators within the DMN, either during meditation (Brewer et al., 2011; Farb et al., 2007) or resting-state (Berkovich-Ohana et al., 2016; Garrison et al., 2013; Hasenkamp & Barsalou, 2012; Kilpatrick et al., 2011; Taylor et al., 2013).

Enhanced resting state FC was shown in the FPN (Froeliger et al., 2012; Hasenkamp & Barsalou, 2012), and the SN (Farb et al., 2013; Hernández et al., 2018). These mindfulness-related FC pattern alterations can be interpreted as reduced mind-wandering and enhanced 'online' attention to representation of body awareness. Several other studies showed enhanced FC between the FPN and SN networks (Farb et al., 2007; Hasenkamp & Barsalou, 2012; Hölzel et al., 2007). Given the important role attributed to the Salience network in switching between FPN and DMN (Sridharan et al., 2008), this can be interpreted to suggest that mindfulness meditators, compared to novices, may have an enhanced awareness of present moment experience and more access to internal bodily states.

Finally, many studies reported altered FC between the DMN and other networks. For example, several studies provided evidence for increased FC between the FPN network and the DMN during both meditation and resting state (Brewer et al., 2011; Creswell et al., 2016; Farb et al., 2007). In other studies, during mindfulness-related meditation, FC between DMN and FPN (Froeliger et al., 2012), SN (Farb et al., 2007), or Somatosensory Network (Berkovich-Ohana et al., 2016; Farb et al., 2007; Josipovic et al., 2012; Kilpatrick et al., 2011) is increased. This can be interpreted to show that during meditation one may have enhanced capacity for disengagement from thought content, and for shifting attention to affective, interoceptive or sensory awareness which can be an indication of enhanced flexibility (Giommi et al., 2023).

Recently, some FC meditation studies have begun to take a dynamic approach (Deco et al., 2011), where the brain is considered to transition between brain states, with different patterns of dynamic FC (DFC, see Box 1) varying in strength. In one study (Escrichs et al., 2019), controls and experienced meditators were scanned using fMRI during resting-state and mindfulness practice. They reported that the dynamical complexity during mindfulness practice showed less complexity than during resting-state in the meditator group but not in the control group. During resting-state, experienced meditators showed higher metastability (i.e., a wider dynamical regime of brain states over time) than the one observed in the control group. These results indicate that in meditators, brain dynamics are more constrained during mindfulness meditation compared to rest, and that meditators' resting brain activity transitions between a larger variety of stable brain states than controls. This is similar to the finding that a dynamical functional connectivity approach has revealed for high trait mindfulness individuals, where increased oscillation between different brain states has been observed (Lim et al., 2018; Marusak et al., 2018). Furthermore, in a case study, it was shown that meditation (1) changed the community size (with a number of regions in the FPN being merged into the DMN after meditation) and (2) led to instability in the community allegiance of the regions in the FPN (Kajimura et al., 2020). These results suggest that, in addition to altering specific FC between brain regions, meditation leads to reconfiguration of whole-brain network architecture.

Another recent study (Panitz et al., 2023) compared dynamic expression of resting state networks over time between long-term mindfulness practitioners and control participants. The analysis uncovered that the meditators at rest tend to spend more time in two brain states that involve cortical regions associated with sensory perception, with a heavy emphasis on visual processing. In contrast, the control participants tend to spend more time in brain state involving areas associated with higher cognitive functions and executive control. These findings suggest that mindfulness meditation might lead to a shift from an emphasis on executive control towards enhanced sensory and embodied processing.

# Discussion

## Research Summary

Sezer, Pizzagalli and Sacchet (2022) reviewed cross-sectional and longitudinal mindfulness studies. First, they found consistent increased connectivity between posterior cingulate cortex (DMN) and dorsolateral prefrontal cortex (FPN) in intervention studies, which may relate to attention control. Second, they found decreased connectivity between cuneus (DMN) and SN, which may relate to self-awareness. This particular result needs further examination, given evidence to the contrary (Bremer et al., 2022; Rahrig et al., 2022). Third, Sezer and colleagues (2022) found decreased connectivity between rostral anterior cingulate cortex region and amygdala regions which may relate to emotion regulation and stress reduction.

The results of our synthesis are largely in line with this review, with a couple additions. The most consistent findings in the triple networks are illustrated in **Figure 3.** The literature supports the possibility of reduced within-DMN connectivity across intervention designs, trait designs, and long-term meditator designs, with implications for decreased mind-wandering and rumination. Second, while interventions may increase DMN-FPN connectivity, the results from trait mindfulness studies (including both static and dynamic functional connectivity) suggest that DMN-FPN may actually be more anticorrelated in more mindful individuals. Differing results in the DMN-FPN may represent methodological differences (as we discuss later), or they could represent different types of functional connectivity - a functional connectivity related to momentary states of mindfulness (DMN-FPN anticorrelations), and a longer time-scale, intrinsic connectivity (DMN-FPN correlations). A third signature is that the dynamic complexity of brain connectivity ***at rest*** may be higher in long-term meditators and more mindful individuals by self-report, as if they occupy a wider range of brain states and thus a wider range of mental experiences.

## Implications for Clinical Treatment

Mindfulness-based interventions (MBIs) have gained considerable attention as transdiagnostic treatments for psychiatric disorders, ranging from anxiety disorders, depression, post-traumatic stress disorder (PTSD), substance use disorders, eating disorders, to borderline personality disorder and schizophrenia (Chadwick et al., 2005; Chiesa & Serretti, 2010; Hofmann et al., 2010; Ivtzan, 2019; Khoury et al., 2013; Vøllestad et al., 2012; Williams et al., 2014). Two meta-analyses of MBIs (Goldberg et al., 2018; Vancampfort et al., 2021) found that mindfulness-based interventions hold promise as evidence-based treatments for psychiatric disorders. The clinical effectiveness of MBIs may be attributed to the underlying brain networks implicated during mindfulness practice that have been reviewed in this chapter (e.g., DMN) which are precisely the same key networks most often implicated in psychiatric disorders.

For example, a recent meta-analysis of resting-state functional magnetic resonance imaging articles published during the last 15 years and comprising observations from more than twenty-five-hundred patients with psychiatric disorders highlights that functional alterations in the major hubs of the DMN are common abnormalities across psychiatric disorders (Doucet et al., 2020). These authors emphasize that DMN abnormalities and associated differences in self-referential mental activity may be transdiagnostic across psychiatric disorders. This is in line with previous hypotheses that have implicated DMN abnormalities and mental disorders (Broyd et al., 2009; Whitfield-Gabrieli et al., 2009; Whitfield-Gabrieli & Ford, 2012). Interestingly, DMN hyperactivation and hyperconnectivity is most often associated with psychopathology, such as rumination, while diminished DMN-CEN anticorrelations are most often associated with cognitive impairment across psychiatric populations (e.g. Zhou et al., 2016).

The clinical benefits of MBIs may be linked to changes in attentional networks like the DMN and CEN. However, there are sparse studies comparing MBIs to active control conditions in clinical groups (Creswell et al., 2016; King et al., 2016; Lifshitz et al., 2019; Taren et al., 2015; for full review see Sezer et al., 2022). One study investigated the effects of MBIs on rsFC in major depression disorder (MDD). Lifshitz and colleagues (2019) compared MDD patients who completed a 2-week mindfulness training program to an active control group of patients who completed a relaxation-based training program. Relative to the active control intervention, participants assigned to mindfulness training exhibited reduced depressive symptoms and improved mindful traits (quantified using the FFMQ). Moreover, mindfulness training was associated with decreased functional connectivity of the FPN, specifically between bilateral DLFPC seeds and bilateral fusiform and right angular gyrus. These regions are involved in top-down processing of sensory input (Dixon et al., 2018) and could be involved in a more mindful self-focus (Freton et al., 2014) and thus shifting away from negative ruminations occurring in MDD.

According to Sezer et al. (2022), MBIs may also alter corticolimbic networks, which may be the reason for an enhancement of emotional regulation and the transdiagnostic benefits that can be observed. In a large-sample study, 130 adults underwent resting-state scans before and after a 3-day intensive mindfulness meditation retreat compared to a matched 3-day relaxation retreat (Taren et al., 2015). At baseline, connectivity between the subgenual-anterior cingulate cortex (sgACC) and amygdala was positively correlated with stress over the last month. This is in accordance with roles for the amygdala and sgACC individually in stress responses (Arnsten, 2009; Gianaros et al., 2008). The 3-day mindfulness retreat decreased sgACC-amygdala connectivity, suggesting a possible pathway for stress reduction in MBIs.

Finally, it is of note that the modulation of MBIs of resting-state networks could have different effects on clinical populations and that there is inconclusive or only preliminary evidence on the effects of MBIs on PTSD, ADHD, ASD and eating disorders. Furthermore, some beneficial effects are not confirmed in subgroup populations. Thus, effectiveness is yet to be confirmed for many health conditions and populations (D. Zhang et al., 2021). In addition, some studies have found potential negative effects. According to the National Center for Complementary and Integrative Health, about 8% of participants may report negative effects from practicing meditation, such as anxiety and depression (*Meditation and Mindfulness*, 2022). However, it is important to note that these negative effects are very rare in standard mindfulness interventions (Hirshberg et al., 2022). MBIs may reflect both an emotional distancing and a reduction in self-referential processing that changes the implicated brain networks (i.e. corticolimbic systems and DMN/FPN). In this sense, MBIs foster a more equanimous, dispositional tendency of mind towards all experiences, with benefits across many psychiatric conditions (Tom & Vago, 2021).

## Limitations and Challenges

Research on functional connectivity and mindfulness is gradually building towards a shared understanding. However, there are inconsistencies in the literature. For example, DMN-FPN correlations seem to increase for mindfulness interventions, and yet anticorrelations between the DMN-FPN are associated with increased trait mindfulness (as well as sustained attention). As another example, while most studies support the possibility of reduced within-DMN connectivity across intervention designs, trait designs, and long-term meditator designs, a recent large sample study found no relationship with trait mindfulness (Hunt et al., 2022). To build a more robust science of mindfulness and fMRI, we suggest three factors need to be considered (1) methods (2) sample sizes, and (3) third variables.

In terms of methods, seed-based FC can be hard to compare across studies because the seed regions chosen vary (Sezer et al., 2022). When investigating DMN connectivity, individuals may choose the precuneus vs the PCC, the dorsal PCC vs the ventral PCC. When investigating frontoparietal network connectivity, individuals may choose dorsolateral PFC vs IPL. It may be the case that there are subcomponents to networks with different functions and anatomical connections etc. (Dixon et al., 2018). This could relate to the inconsistent findings with regards to DMN-FPN connectivity. On the other hand, ICA methods don’t require hypotheses about network functions. However, the networks extracted by ICA may blend across heterogeneous regions of the brain, and may hard to be categorize as ‘visual’ or ‘attentional’ etc.

Another challenge with regards to methods is that the order of fMRI scans may introduce biases (Grigg & Grady, 2010), although systematic inquiry is in its infancy. Resting-state after meditation may be contaminated and not represent true ‘rest’, and long-term practitioners may meditate intentionally or unintentionally during rest. Tasks before or after resting state may likewise introduce biases. Indicator variables relating to these orders could be introduced into meta-analyses to see if order systematically biases connectivity results.

Moving on, it is increasingly evident that fMRI studies require large sample sizes. For example, a recent review found that brain-behavior/self-report correlations may require hundreds if not thousands of individuals (Marek et al., 2022), perhaps due to low within-individual reliability in both the brain measure and behavioral/self-report measure. Most of the studies reviewed here have <100 subjects. Especially in the study of trait mindfulness, this is a concern.

fMRI studies of mindfulness should embrace big data. For looking at individual differences, big 'wide' data is a necessity. For looking at state mindfulness within-individuals (e.g., what happens when you practice), big 'deep' data should also be encouraged. For example, Weng et al. (2020) had a small sample of 8 meditators and 8 naive participants perform different types of meditation practices in the scanner. With over 432 datapoints (TR:1.0s, total duration ~ 7 minutes) from each practice from each individual, they could train a classifier to decode which meditation the participants were performing. They showed that this classifier performed above chance in all 8 meditators, and 6 of 8 non-meditators, but the patterns contributing to the classification varied greatly.

Lastly, third variables like age, gender, socioeconomic status (SES), etc. may have overlooked effects on the relationship between mindfulness and functional connectivity. A recent study by Ellwood-Lowe et al. (2021) in a sample of over 6,000 individuals found that cognitive task performance correlated with FPN-DMN anticorrelations assessed during resting-state for individuals who were high in SES, but the pattern reversed in low SES individuals. This could inherently be because the network couplings differ, or it could be that the brain networks used in connectivity analyses are biased in a hidden way (e.g., applying a DMN mask first derived in high SES groups to low SES captures another network). Either way, brain network organization is meaningfully distinct, but in nuanced ways. We suggest that researchers try to control for third variables (keeping in mind that collinearity can interfere with regression analyses), and additionally, look into different ways of defining the networks (e.g., MELODIC vs GroupICA) for specifying different assumptions about how networks vary across individuals.

## Future Directions

A brain network science of mindfulness can help us understand what makes some individuals more mindful than others, what changes during a mindfulness intervention, and what happens in the moment of mindfulness meditation. In addition to these fundamental questions, this research has implications for neuromodulation. In neuromodulation, researchers develop a specific hypothesis about brain functions or responses (e.g., DMN activations promote mind-wandering), and they use that hypothesis to intervene (e.g., decreasing activations in the DMN). One new type of neuromodulation research is real-time fMRI neurofeedback (rt-fMRI). In this paradigm, participants watch their brain activity on a screen while performing a task. They are then able to tailor their strategies during the task to modulate their brain activity. For example, real-time neurofeedback can be provided to augment mindfulness skill acquisition in healthy individuals as well as individuals suffering from psychosis, anxiety and/or depression (Bauer, Okano, et al., 2020; Okano et al., 2020; J. Zhang et al., 2023). Participants first undergo a resting-state scan, and spatial independent component analysis (ICA) is run on the scans to functionally localize each individual's precise DMN and FPN. Participants viewed a visual display of their real time brain activity (a "mental mirror") and were asked to move a ball up by practicing mindfulness (*open monitoring* – nonreactively noticing thoughts and sensations in the present moment). Mindfulness enables the participants to volitionally reduce their DMN activation relative to their FPN activation (DMN< FPN), however the ball moves down when the participants start to engage in mind wandering (DMN>FPN). Participants are instructed that if they are practicing the meditation correctly, the ball will move up (corresponding to DMN < FPN). These studies have found that the neurofeedback may reduce auditory hallucinations in patients with schizophrenia by normalizing DMN connectivity with other brain regions, and increase self-reported state mindfulness.

Mindfulness based rt-fMRI neurofeedback interventions can be non-invasive, personalized, potentially transformative circuit therapies for individuals suffering from mental illness, as well as children at-risk for developing mental disorders. Neurofeedback offers an unprecedented opportunity to train individuals to volitionally down regulate their DMN and subsequently mitigate debilitating symptoms that often lead to a diminished quality of life.

The rt-fMRI method also allows researchers to investigate the neural correlates of subjective experience in real-time (Garrison et al., 2013) and gain insight into first person states of mind during meditation. For example, Garrison et al. (2013) used rt-fMRI to investigate the correlates of posterior cingulate cortex (PCC) activity (a mayor hub of the DMN) in meditators' self-report and found that PCC deactivation is correlated with the subjective feelings of "undistracted awareness" in meditators, such as being "concentrated" and "observing sensory experience," as well as "effortless doing," which includes "observing sensory experience," "not efforting," and "contentment." On the contrary, feelings like "efforting" and "discontentment," as well as "distracted awareness" experiences like "distraction" and "interpreting," were found to be correlated with increased PCC activity. This novel technique based on first-person accounts, could further provide unique insights into the dynamics of brain activity and connectivity during meditation and its relationship to mind wandering or self-related thinking. Furthermore, it could provide a personalized roadmap to finding the best practice for any individual and or help overcome hurdles during the process of learning to meditate.

Finally, to measure and target the major brain regions and networks that are involved during meditation, current methods rely heavily on fMRI technology, which is an expensive procedure involving a complex setup and patient burden. Fortunately, frequency-specific components of electroencephalography (EEG) signals recorded on the scalp can serve as correlates of fMRI activity patterns, including DMN activity and connectivity (Bocharov et al., 2023; Van Lutterveld et al., 2017). One way to make this research more accessible is to validate the EEG correlates of brain interactions implicated during meditation using concurrent EEG-fMRI and to develop specific EEG “fingerprints” (Meir-Hasson et al., 2014) of these fMRI brain areas and network dynamics in order to take this technology out of the MRI environment and into a more naturalistic environment. Ultimately, one could imagine a scalable, technology-based training platform that augments mindfulness skill acquisition and utilization in healthy individuals as well as supports individuals suffering from mental illness.

## References

Adelman, G. (1987). *Encyclopedia of neuroscience*. Birkhäuser.

Allen, E. A., Damaraju, E., Plis, S. M., Erhardt, E. B., Eichele, T., & Calhoun, V. D. (2014). Tracking whole-brain connectivity dynamics in the resting state. *Cerebral Cortex*, *24*(3), 663–676.

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature reviews neuroscience*, *7*(4), 268-277.

Andrews-Hanna, J. R., Reidler, J. S., Sepulcre, J., Poulin, R., & Buckner, R. L. (2010). Functional-anatomic fractionation of the brain’s default network. *Neuron*, *65*(4), 550–562.

Arnsten, A. F. (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nature Reviews Neuroscience*, *10*(6), 410–422.

Baer, R. A., Smith, G. T., Hopkins, J., Krietemeyer, J., & Toney, L. (2006). Using self-report assessment methods to explore facets of mindfulness. *Assessment*, *13*(1), 27–45.

Bandettini, P. A., Jesmanowicz, A., Wong, E. C., & Hyde, J. S. (1993). Processing strategies for time-course data sets in functional MRI of the human brain. *Magnetic resonance in medicine*, *30*(2), 161-173.

Bauer, C. C. C., Whitfield-Gabrieli, S., Díaz, J. L., Pasaye, E. H., & Barrios, F. A. (2019). From state-to-trait meditation: Reconfiguration of central executive and default mode networks. *Eneuro*, *6*(6).

Bauer, C. C., Okano, K., Ghosh, S. S., Lee, Y. J., Melero, H., de Los Angeles, C., Nestor, P. G., Del Re, E. C., Northoff, G., & Niznikiewicz, M. A. (2020). Real-time fMRI neurofeedback reduces auditory hallucinations and modulates resting state connectivity of involved brain regions: Part 2: Default mode network-preliminary evidence. *Psychiatry Research*, *284*, 112770.

Bauer, C. C., Rozenkrantz, L., Caballero, C., Nieto-Castanon, A., Scherer, E., West, M. R., Mrazek, M., Phillips, D. T., Gabrieli, J. D., & Whitfield-Gabrieli, S. (2020). Mindfulness training preserves sustained attention and resting state anticorrelation between default-mode network and dorsolateral prefrontal cortex: A randomized controlled trial. *Human Brain Mapping*, *41*(18), 5356–5369.

Berkovich-Ohana, A., Harel, M., Hahamy, A., Arieli, A., & Malach, R. (2016). Data for default network reduced functional connectivity in meditators, negatively correlated with meditation expertise. *Data in Brief, 8,* 910–914.

Bilevicius, E., Smith, S. D., & Kornelsen, J. (2018). Resting-state network functional connectivity patterns associated with the Mindful Attention Awareness Scale. *Brain Connectivity*, *8*(1), 40–48.

Biswal, B., Zerrin Yetkin, F., Haughton, V. M., & Hyde, J. S. (1995). Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. *Magnetic Resonance in Medicine*, *34*(4), 537–541.

Bocharov, A. V., Savostyanov, A. N., Tamozhnikov, S. S., Karpova, A. G., Milakhina, N. S., Zavarzin, E. A., Saprigyn, A. E., & Knyazev, G. G. (2023). Electrophysiological signatures of resting state networks under new environmental conditions. *Neuroscience Letters*, *794*, 137012.

Brefczynski-Lewis, J. A., Lutz, A., Schaefer, H. S., Levinson, D. B., & Davidson, R. J. (2007). Neural correlates of attentional expertise in long-term meditation practitioners. *Proceedings of the National Academy of Sciences*, *104*(27), 11483–11488. https://doi.org/10.1073/pnas.0606552104

Bremer, B., Wu, Q., Mora Álvarez, M. G., Hölzel, B. K., Wilhelm, M., Hell, E., Tavacioglu, E. E., Torske, A., & Koch, K. (2022). Mindfulness meditation increases default mode, salience, and central executive network connectivity. *Scientific Reports*, *12*(1), 13219.

Bressler, S. L. (1995). Large-scale cortical networks and cognition. *Brain Research Reviews*, *20*(3), 288–304.

Brewer, J. A., Worhunsky, P. D., Gray, J. R., Tang, Y.-Y., Weber, J., & Kober, H. (2011). Meditation experience is associated with differences in default mode network activity and connectivity. *Proceedings of the National Academy of Sciences*, *108*(50), 20254–20259.

Brown, K. W., & Ryan, R. M. (2003). The benefits of being present: Mindfulness and its role in psychological well-being. *Journal of Personality and Social Psychology*, *84*(4), 822–848. https://doi.org/10.1037/0022-3514.84.4.822

Broyd, S. J., Demanuele, C., Debener, S., Helps, S. K., James, C. J., & Sonuga-Barke, E. J. (2009). Default-mode brain dysfunction in mental disorders: A systematic review. *Neuroscience & Biobehavioral Reviews*, *33*(3), 279–296.

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, *1124*(1), 1–38.

Bzdok, D., Laird, A. R., Zilles, K., Fox, P. T., & Eickhoff, S. B. (2013). An investigation of the structural, connectional, and functional subspecialization in the human amygdala. *Human brain mapping*, *34*(12), 3247-3266.

Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: an attentional account. *Nature reviews neuroscience*, *9*(8), 613-625.

Calhoun, V. D., Adali, T., Pearlson, G. D., & Pekar, J. J. (2001). A method for making group inferences from functional MRI data using independent component analysis. *Human brain mapping*, *14*(3), 140-151.

Chadwick, P., Taylor, K. N., & Abba, N. (2005). Mindfulness groups for people with psychosis. *Behavioural and Cognitive Psychotherapy*, *33*(3), 351–359.

Chen, K., Azeez, A., Chen, D. Y., & Biswal, B. B. (2020). Resting-state functional connectivity: Signal origins and analytic methods. *Neuroimaging Clinics*, *30*(1), 15–23.

Chiesa, A., & Serretti, A. (2010). A systematic review of neurobiological and clinical features of mindfulness meditations. *Psychological Medicine*, *40*(8), 1239–1252.

Christoff, K., Gordon, A. M., Smallwood, J., Smith, R., & Schooler, J. W. (2009). Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. *Proceedings of the National Academy of Sciences*, *106*(21), 8719–8724. https://doi.org/10.1073/pnas.0900234106

Chumachenko, S. Y., Cali, R. J., Rosal, M. C., Allison, J. J., Person, S. J., Ziedonis, D., Nephew, B. C., Moore, C. M., Zhang, N., King, J. A., & Fulwiler, C. (2021). Keeping weight off: Mindfulness-Based Stress Reduction alters amygdala functional connectivity during weight loss maintenance in a randomized control trial. *PLOS ONE*, *16*(1), e0244847. https://doi.org/10.1371/journal.pone.0244847

Cole, M. W., Reynolds, J. R., Power, J. D., Repovs, G., Anticevic, A., & Braver, T. S. (2013). Multi-task connectivity reveals flexible hubs for adaptive task control. *Nature neuroscience*, *16*(9), 1348-1355.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron*, *58*(3), 306–324.

Creswell, J. D., Taren, A. A., Lindsay, E. K., Greco, C. M., Gianaros, P. J., Fairgrieve, A., Marsland, A. L., Brown, K. W., Way, B. M., & Rosen, R. K. (2016). Alterations in resting-state functional connectivity link mindfulness meditation with reduced interleukin-6: A randomized controlled trial. *Biological Psychiatry*, *80*(1), 53–61.

Deco, G., Jirsa, V. K., & McIntosh, A. R. (2011). Emerging concepts for the dynamical organization of resting-state activity in the brain. *Nature Reviews Neuroscience*, *12*(1), 43–56.

Dixon, M. L., Andrews-Hanna, J. R., Spreng, R. N., Irving, Z. C., Mills, C., Girn, M., & Christoff, K. (2017). Interactions between the default network and dorsal attention network vary across default subsystems, time, and cognitive states. *Neuroimage*, *147*, 632–649.

Dixon, M. L., De La Vega, A., Mills, C., Andrews-Hanna, J., Spreng, R. N., Cole, M. W., & Christoff, K. (2018). Heterogeneity within the frontoparietal control network and its relationship to the default and dorsal attention networks. *Proceedings of the National Academy of Sciences*, *115*(7), E1598–E1607.

Doll, A., Hölzel, B. K., Boucard, C. C., Wohlschläger, A. M., & Sorg, C. (2015). Mindfulness is associated with intrinsic functional connectivity between default mode and salience networks. *Frontiers in Human Neuroscience*, *9*, 461.

Doucet, G. E., Janiri, D., Howard, R., O'Brien, M., Andrews-Hanna, J. R., & Frangou, S. (2020). Transdiagnostic and disease-specific abnormalities in the default-mode network hubs in psychiatric disorders: A meta-analysis of resting-state functional imaging studies. *European Psychiatry*, *63*(1), e57.

Drevets, W. C., Price, J. L., & Furey, M. L. (2008). Brain structural and functional abnormalities in mood disorders: implications for neurocircuitry models of depression. *Brain structure and function*, *213*, 93-118.

Drevets, W. C., & Raichle, M. E. (1998). Reciprocal suppression of regional cerebral blood flow during emotional versus higher cognitive processes: Implications for interactions between emotion and cognition. *Cognition and emotion*.

Ellwood-Lowe, M. E., Whitfield-Gabrieli, S., & Bunge, S. A. (2021). Brain network coupling associated with cognitive performance varies as a function of a child's environment in the ABCD study. *Nature Communications*, *12*(1), 7183. https://doi.org/10.1038/s41467-021-27336-y

Escrichs, A., Sanjuán, A., Atasoy, S., López-González, A., Garrido, C., Càmara, E., & Deco, G. (2019). Characterizing the dynamical complexity underlying meditation. *Frontiers in Systems Neuroscience*, *13*, 27.

Farb, N. A., Segal, Z. V., & Anderson, A. K. (2013). Mindfulness meditation training alters cortical representations of interoceptive attention. *Social Cognitive and Affective Neuroscience*, *8*(1), 15–26.

Farb, N. A., Segal, Z. V., Mayberg, H., Bean, J., McKeon, D., Fatima, Z., & Anderson, A. K. (2007). Attending to the present: Mindfulness meditation reveals distinct neural modes of self-reference. *Social Cognitive and Affective Neuroscience*, *2*(4), 313–322.

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences*, *102*(27), 9673–9678. https://doi.org/10.1073/pnas.0504136102

Fransson, P., & Marrelec, G. (2008). The precuneus/posterior cingulate cortex plays a pivotal role in the default mode network: Evidence from a partial correlation network analysis. *Neuroimage*, *42*(3), 1178–1184.

Freton, M., Lemogne, C., Delaveau, P., Guionnet, S., Wright, E., Wiernik, E., Bertasi, E., & Fossati, P. (2014). The dark side of self-focus: Brain activity during self-focus in low and high brooders. *Social Cognitive and Affective Neuroscience*, *9*(11), 1808–1813.

Friston, K. J., Frith, C. D., Frackowiak, R. S., & Turner, R. (1995). Characterizing dynamic brain responses with fMRI: a multivariate approach. *Neuroimage*, *2*(2), 166-172.

Friston, K. J., Frith, C. D., Liddle, P. F., & Frackowiak, R. S. (1993). Functional connectivity: The principal-component analysis of large (PET) data sets. *Journal of Cerebral Blood Flow & Metabolism, 13*(1), 5–14.

Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. P., Frith, C. D., & Frackowiak, R. S. (1994). Statistical parametric maps in functional imaging: a general linear approach. *Human brain mapping*, *2*(4), 189-210.

Froeliger, B., Garland, E. L., Kozink, R. V., Modlin, L. A., Chen, N.-K., McClernon, F. J., Greeson, J. M., & Sobin, P. (2012). Meditation-state functional connectivity (msFC): Strengthening of the dorsal attention network and beyond. *Evidence-Based Complementary and Alternative Medicine*, *2012*.

Gan, Q., Ding, N., Bi, G., Liu, R., Zhao, X., Zhong, J., Wu, S., Zeng, Y., Cui, L., Wu, K., Fu, Y., & Chen, Z. (2022). Enhanced Resting-State Functional Connectivity With Decreased Amplitude of Low-Frequency Fluctuations of the Salience Network in Mindfulness Novices. *Frontiers in Human Neuroscience*, *16*, 838123. https://doi.org/10.3389/fnhum.2022.838123

Ganesan, S., Beyer, E., Moffat, B., Van Dam, N. T., Lorenzetti, V., & Zalesky, A. (2022). Focused attention meditation in healthy adults: A systematic review and meta-analysis of cross-sectional functional MRI studies. *Neuroscience & Biobehavioral Reviews*, 104846.

Garrison, K. A., Santoyo, J. F., Davis, J. H., Thornhill IV, T. A., Kerr, C. E., & Brewer, J. A. (2013). Effortless awareness: Using real time neurofeedback to investigate correlates of posterior cingulate cortex activity in meditators’ self-report. *Frontiers in Human Neuroscience*, *7*, 440.

Garrison, K. A., Zeffiro, T. A., Scheinost, D., Constable, R. T., & Brewer, J. A. (2015). Meditation leads to reduced default mode network activity beyond an active task. *Cognitive, Affective, & Behavioral Neuroscience, 15*, 712–720.

Geschwind, N. (1974). Disconnexion Syndromes in Animals and Man. In R. S. Cohen & M. W. Wartofsky (Eds.), *Selected Papers on Language and the Brain* (Vol. 16, pp. 105–236). Springer Netherlands. https://doi.org/10.1007/978-94-010-2093-0_8

Gianaros, P. J., Sheu, L. K., Matthews, K. A., Jennings, J. R., Manuck, S. B., & Hariri, A. R. (2008). Individual differences in stressor-evoked blood pressure reactivity vary with activation, volume, and functional connectivity of the amygdala. *Journal of Neuroscience, 28*(4), 990–999.

Giommi, F., Bauer, P. R., Berkovich-Ohana, A., Barendregt, H., Brown, K. W., Gallagher, S., Nyklíček, I., Ostafin, B., Raffone, A., & Slagter, H. A. (2023). The (In) flexible self: Psychopathology, mindfulness, and neuroscience. *International Journal of Clinical and Health Psychology, 23*(4), 100381.

Goldberg, S. B., Riordan, K. M., Sun, S., & Davidson, R. J. (2022). The Empirical Status of Mindfulness-Based Interventions: A Systematic Review of 44 Meta-Analyses of Randomized Controlled Trials. *Perspectives on Psychological Science, 17*(1), 108–130. https://doi.org/10.1177/1745691620968771

Goldberg, S. B., Tucker, R. P., Greene, P. A., Davidson, R. J., Wampold, B. E., Kearney, D. J., & Simpson, T. L. (2018). Mindfulness-based interventions for psychiatric disorders: A systematic review and meta-analysis. *Clinical Psychology Review, 59*, 52–60.

Goswami, R., Frances, M. F., & Shoemaker, J. K. (2011). Representation of somatosensory inputs within the cortical autonomic network. *Neuroimage, 54*(2), 1211-1220.

Greicius, M. D., Srivastava, G., Reiss, A. L., & Menon, V. (2004). Default-mode network activity distinguishes Alzheimer's disease from healthy aging: Evidence from functional MRI. *Proceedings of the National Academy of Sciences*, *101*(13), 4637–4642.

Grigg, O., & Grady, C. L. (2010). Task-related effects on the temporal and spatial dynamics of resting-state functional connectivity in the default network. *PloS One*, *5*(10), e13311.

Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience*, *2*(10), 685–694.

Hampson, M., Olson, I. R., Leung, H.-C., Skudlarski, P., & Gore, J. C. (2004). Changes in functional connectivity of human MT/V5 with visual motion input. *Neuroreport*, *15*(8), 1315–1319.

Hampson, M., Peterson, B. S., Skudlarski, P., Gatenby, J. C., & Gore, J. C. (2002). Detection of functional connectivity using temporal correlations in MR images. *Human Brain Mapping*, *15*(4), 247–262.

Harrison, R., Zeidan, F., Kitsaras, G., Ozcelik, D., & Salomons, T. V. (2019). Trait mindfulness is associated with lower pain reactivity and connectivity of the default mode network. *The Journal of Pain*, *20*(6), 645–654.

Hasenkamp, W., & Barsalou, L. W. (2012). Effects of meditation experience on functional connectivity of distributed brain networks. *Frontiers in Human Neuroscience*, *6*, 38.

Hasenkamp, W., Wilson-Mendenhall, C. D., Duncan, E., & Barsalou, L. W. (2012). Mind wandering and attention during focused meditation: A fine-grained temporal analysis of fluctuating cognitive states. *Neuroimage*, *59*(1), 750–760.

Hellyer, P. J., Shanahan, M., Scott, G., Wise, R. J. S., Sharp, D. J., & Leech, R. (2014). The Control of Global Brain Dynamics: Opposing Actions of Frontoparietal Control and

Default Mode Networks on Attention. *The Journal of Neuroscience*, *34*(2), 451–461. https://doi.org/10.1523/JNEUROSCI.1853-13.2014

Hernández, S. E., Barros-Loscertales, A., Xiao, Y., Gonzalez-Mora, J. L., & Rubia, K. (2018). Gray matter and functional connectivity in anterior cingulate cortex are associated with the state of mental silence during sahaja yoga meditation. *Neuroscience*, *371*, 395–406.

Hirshberg, M. J., Goldberg, S. B., Rosenkranz, M., & Davidson, R. J. (2022). Prevalence of harm in mindfulness-based stress reduction. *Psychological Medicine*, *52*(6), 1080–1088.

Hofmann, S. G., Sawyer, A. T., Witt, A. A., & Oh, D. (2010). The effect of mindfulness-based therapy on anxiety and depression: A meta-analytic review. *Journal of Consulting and Clinical Psychology*, *78*(2), 169.

Hölzel, B. K., Ott, U., Hempel, H., Hackl, A., Wolf, K., Stark, R., & Vaitl, D. (2007). Differential engagement of anterior cingulate and adjacent medial frontal cortex in adept meditators and non-meditators. *Neuroscience Letters*, *421*(1), 16–21.

Hunt, C. A., Letzen, J. E., Krimmel, S. R., Burrowes, S. A., Haythornthwaite, J. A., Finan, P. H., Vetter, M., & Seminowicz, D. A. (2022). Is mindfulness associated with lower pain reactivity and connectivity of the default mode network? A replication and extension study in healthy and episodic migraine participants. *The Journal of Pain*, *23*(12), 2110–2120.

Hutchison, R. M., Womelsdorf, T., Allen, E. A., Bandettini, P. A., Calhoun, V. D., Corbetta, M., ... & Chang, C. (2013). Dynamic functional connectivity: promise, issues, and interpretations. *Neuroimage*, *80*, 360-378.

Hyvärinen, A., & Oja, E. (2000). Independent component analysis: algorithms and applications. *Neural networks*, *13*(4-5), 411-430.

Ivtzan, I. (2019). *Handbook of mindfulness-based programmes: Mindfulness interventions from education to health and therapy*. Routledge.

Jang, J. H., Jung, W. H., Kang, D.-H., Byun, M. S., Kwon, S. J., Choi, C.-H., & Kwon, J. S. (2011). Increased default mode network connectivity associated with meditation. *Neuroscience Letters*, *487*(3), 358–362.

Josipovic, Z., Dinstein, I., Weber, J., & Heeger, D. J. (2012). Influence of meditation on anti-correlated networks in the brain. *Frontiers in Human Neuroscience*, *5*, 183.

Kajimura, S., Masuda, N., Lau, J. K. L., & Murayama, K. (2020). Focused attention meditation changes the boundary and configuration of functional networks in the brain. *Scientific Reports*, *10*(1), 1–11.

Kandel, E. R., Schwartz, J. H., Jessell, T. M., Siegelbaum, S., Hudspeth, A. J., & Mack, S. (2000). *Principles of neural science* (Vol. 4). McGraw-hill New York.

Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the Self? An Event-Related fMRI Study. *Journal of Cognitive Neuroscience*, *14*(5), 785–794. https://doi.org/10.1162/08989290260138672

Khoury, B., Lecomte, T., Fortin, G., Masse, M., Therien, P., Bouchard, V., Chapleau, M.-A., Paquin, K., & Hofmann, S. G. (2013). Mindfulness-based therapy: A comprehensive meta-analysis. *Clinical Psychology Review*, *33*(6), 763–771.

Kilpatrick, L. A., Suyenobu, B. Y., Smith, S. R., Bueller, J. A., Goodman, T., Creswell, J. D., Tillisch, K., Mayer, E. A., & Naliboff, B. D. (2011). Impact of mindfulness-based stress reduction training on intrinsic brain connectivity. *Neuroimage*, *56*(1), 290–298.

King, A. P., Block, S. R., Sripada, R. K., Rauch, S., Giardino, N., Favorite, T., Angstadt, M., Kessler, D., Welsh, R., & Liberzon, I. (2016). Altered default mode network (DMN) resting state functional connectivity following a mindfulness-based exposure therapy for posttraumatic stress disorder (PTSD) in combat veterans of Afghanistan and Iraq. *Depression and Anxiety*, *33*(4), 289–299.

Kong, F., Wang, X., Song, Y., & Liu, J. (2016). Brain regions involved in dispositional mindfulness during resting state and their relation with well-being. *Social Neuroscience*, *11*(4), 331–343. https://doi.org/10.1080/17470919.2015.1092469

Kral, T. R., Imhoff-Smith, T., Dean III, D. C., Grupe, D., Adluru, N., Patsenko, E., Mumford, J. A., Goldman, R., Rosenkranz, M. A., & Davidson, R. J. (2019). Mindfulness-based stress reduction-related changes in posterior cingulate resting brain connectivity. *Social Cognitive and Affective Neuroscience*, *14*(7), 777–787.

Kucyi, A. (2018). Just a thought: How mind-wandering is represented in dynamic brain connectivity. *Neuroimage*, *180*, 505–514.

Kwak, S., Lee, T. Y., Jung, W. H., Hur, J.-W., Bae, D., Hwang, W. J., Cho, K. I. K., Lim, K.-O., Kim, S.-Y., Park, H. Y., & Kwon, J. S. (2019). The Immediate and Sustained Positive Effects of Meditation on Resilience Are Mediated by Changes in the Resting Brain. *Frontiers in Human Neuroscience*, *13*, 101. https://doi.org/10.3389/fnhum.2019.00101

Levinson, D. B., Stoll, E. L., Kindy, S. D., Merry, H. L., & Davidson, R. J. (2014). A mind you can count on: Validating breath counting as a behavioral measure of mindfulness. *Frontiers in Psychology*, *5*, 1202.

Li, J., Chen, Y., Zheng, J., & Qiu, J. (2022). Dispositional mindfulness and self-referential neural activity during the resting state. *Social Neuroscience*, *17*(1), 13–20. https://doi.org/10.1080/17470919.2021.2009559

Lifshitz, M., Sacchet, M. D., Huntenburg, J. M., Thiery, T., Fan, Y., Gärtner, M., Grimm, S., Winnebeck, E., Fissler, M., & Schroeter, T. A. (2019). Mindfulness-based therapy regulates brain connectivity in major depression. *Psychotherapy and Psychosomatics*, *88*(6), 375–377.

Lim, J., Teng, J., Patanaik, A., Tandi, J., & Massar, S. A. (2018). Dynamic functional connectivity markers of objective trait mindfulness. *Neuroimage*, *176*, 193–202.

Logothetis, N. K., & Pfeuffer, J. (2004). On the nature of the BOLD fMRI contrast mechanism. *Magnetic resonance imaging*, *22*(10), 1517-1531.

Lowe, M. J., Mock, B. J., & Sorenson, J. A. (1998). Functional Connectivity in Single and Multislice Echoplanar Imaging Using Resting-State Fluctuations. *NeuroImage*, *7*(2), 119–132. https://doi.org/10.1006/nimg.1997.0315

Lutz, A., Slagter, H. A., Dunne, J. D., & Davidson, R. J. (2008). Attention regulation and monitoring in meditation. *Trends in Cognitive Sciences*, *12*(4), 163–169.

Maglione, M. A., Maher, A. R., Ewing, B., Colaiaco, B., Newberry, S., Kandrack, R., Shanman, R. M., Sorbero, M. E., & Hempel, S. (2017). Efficacy of mindfulness meditation for smoking cessation: A systematic review and meta-analysis. *Addictive Behaviors*, *69*, 27–34.

Manna, A., Raffone, A., Perrucci, M. G., Nardo, D., Ferretti, A., Tartaro, A., Londei, A., Del Gratta, C., Belardinelli, M. O., & Romani, G. L. (2010). Neural correlates of focused attention and cognitive monitoring in meditation. *Brain Research Bulletin*, *82*(1–2), 46–56. https://doi.org/10.1016/j.brainresbull.2010.03.001

Marek, S., Tervo-Clemmens, B., Calabro, F. J., Montez, D. F., Kay, B. P., Hatoum, A. S., Donohue, M. R., Foran, W., Miller, R. L., Hendrickson, T. J., Malone, S. M., Kandala, S., Feczko, E., Miranda-Dominguez, O., Graham, A. M., Earl, E. A., Perrone, A. J., Cordova, M., Doyle, O., … Dosenbach, N. U. F. (2022). Reproducible brain-wide association studies require thousands of individuals. *Nature*, *603*(7902), 654–660. https://doi.org/10.1038/s41586-022-04492-9

Martinez-Gutierrez, E., Jimenez-Marin, A., Stramaglia, S., & Cortes, J. M. (2022). The structure of anticorrelated networks in the human brain. *Frontiers in Network Physiology*, *2*, 946380. https://doi.org/10.3389/fnetp.2022.946380

Marusak, H. A., Elrahal, F., Peters, C. A., Kundu, P., Lombardo, M. V., Calhoun, V. D., Goldberg, E. K., Cohen, C., Taub, J. W., & Rabinak, C. A. (2018). Mindfulness and dynamic functional neural connectivity in children and adolescents. *Behavioural Brain Research*, *336*, 211–218.

*Meditation and Mindfulness: What You Need To Know*. (2022, June). NCCIH. https://www.nccih.nih.gov/health/meditation-and-mindfulness-what-you-need-to-know

Meir-Hasson, Y., Kinreich, S., Podlipsky, I., Hendler, T., & Intrator, N. (2014). An EEG finger-print of fMRI deep regional activation. *Neuroimage*, *102*, 128–141.

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: a network model of insula function. *Brain structure and function*, *214*, 655-667.

Mesulam, M.-M. (1990). Large-scale neurocognitive networks and distributed processing for attention, language, and memory. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, *28*(5), 597–613.

Mooneyham, B. W., Mrazek, M. D., Mrazek, A. J., Mrazek, K. L., Phillips, D. T., & Schooler, J. W. (2017). States of mind: Characterizing the neural bases of focus and mind-wandering through dynamic functional connectivity. *Journal of Cognitive Neuroscience*, *29*(3), 495–506.

Mrazek, M. D., Smallwood, J., & Schooler, J. W. (2012). Mindfulness and mind-wandering: Finding convergence through opposing constructs. *Emotion*, *12*(3), 442.

Northoff, G., Heinzel, A., De Greck, M., Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain—A meta-analysis of imaging studies on the self. *NeuroImage*, *31*(1), 440–457. https://doi.org/10.1016/j.neuroimage.2005.12.002

Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Sciences*, *9*(5), 242–249.

Ogawa, S., Lee, T. M., Kay, A. R., & Tank, D. W. (1990). Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *proceedings of the National Academy of Sciences*, *87*(24), 9868-9872.

Ogawa, S., Tank, D. W., Menon, R., Ellermann, J. M., Kim, S. G., Merkle, H., & Ugurbil, K. (1992). Intrinsic signal changes accompanying sensory stimulation: Functional brain mapping with magnetic resonance imaging. *Proceedings of the National Academy of Sciences*, *89*(13), 5951–5955.

Okano, K., Bauer, C. C. C., Ghosh, S. S., Lee, Y. J., Melero, H., de los Angeles, C., Nestor, P. G., del Re, E. C., Northoff, G., Whitfield-Gabrieli, S., & Niznikiewicz, M. A. (2020). Real-time fMRI feedback impacts brain activation, results in auditory hallucinations reduction: Part 1: Superior temporal gyrus -Preliminary evidence-. *Psychiatry Research*, *286*, 112862. https://doi.org/10.1016/j.psychres.2020.112862

Panitz, D. Y., Mendelsohn, A., Cabral, J., & Berkovitch-Ohana, A. (2023). Long-term mindfulness meditators exhibit increased spontaneous occurrence of brain states involving sensory and attention networks. *Preprint*.

Parkinson, T. D., Kornelsen, J., & Smith, S. D. (2019). Trait Mindfulness and Functional Connectivity in Cognitive and Attentional Resting State Networks. *Frontiers in Human Neuroscience*, *13*, 112. https://doi.org/10.3389/fnhum.2019.00112

Rahrig, H., Vago, D. R., Passarelli, M. A., Auten, A., Lynn, N. A., & Brown, K. W. (2022). Meta-analytic evidence that mindfulness training alters resting state default mode network connectivity. *Scientific Reports*, *12*(1), 12260. https://doi.org/10.1038/s41598-022-15195-6

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(2), 676–682. https://doi.org/10.1073/pnas.98.2.676

Raichle, M. E., & Snyder, A. Z. (2007). A default mode of brain function: A brief history of an evolving idea. *Neuroimage*, *37*(4), 1083–1090.

Ramón y Cajal, S. (1990). *New Ideas on the Structure of the Nervous System in Man and Vertebrates*. MIT Press.

Rumelhart, D. E., Hinton, G. E., & McClelland, J. L. (1986). A general framework for parallel distributed processing. *Parallel Distributed Processing: Explorations in the Microstructure of Cognition*, *1*(45–76), 26.

Sajonz, B., Kahnt, T., Margulies, D. S., Park, S. Q., Wittmann, A., Stoy, M., Ströhle, A., Heinz, A., Northoff, G., & Bermpohl, F. (2010). Delineating self-referential processing from episodic memory retrieval: Common and dissociable networks. *NeuroImage*, *50*(4), 1606–1617. https://doi.org/10.1016/j.neuroimage.2010.01.087

Scharnowski, F., Veit, R., Zopf, R., Studer, P., Bock, S., Diedrichsen, J., ... & Weiskopf, N. (2015). Manipulating motor performance and memory through real-time fMRI neurofeedback. *Biological psychology*, *108*, 85-97.

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Reiss, A. L., & Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *Journal of Neuroscience*, *27*(9), 2349–2356.

Sezer, I., Pizzagalli, D. A., & Sacchet, M. D. (2022). Resting-state fMRI functional connectivity and mindfulness in clinical and non-clinical contexts: A review and synthesis. *Neuroscience & Biobehavioral Reviews*, 104583.

Shao, R., Keuper, K., Geng, X., & Lee, T. M. C. (2016). Pons to Posterior Cingulate Functional Projections Predict Affective Processing Changes in the Elderly Following Eight Weeks of Meditation Training. *EBioMedicine*, *10*, 236–248. https://doi.org/10.1016/j.ebiom.2016.06.018

Shaurya Prakash, R., De Leon, A. A., Klatt, M., Malarkey, W., & Patterson, B. (2013). Mindfulness disposition and default-mode network connectivity in older adults. *Social Cognitive and Affective Neuroscience*, *8*(1), 112–117.

Smith, E. S. (1971). Galen on the Usefulness of the Parts of the Body (Peri Chreias Morion. De usu partium). Margaret Tallmadge May. *Isis*, *62*(4), 540–542. https://doi.org/10.1086/350814

Sporns, O. (2011). The human connectome: a complex network. *Annals of the new York Academy of Sciences*, *1224*(1), 109-125.

Sporns, O. (2013). Network attributes for segregation and integration in the human brain. *Current opinion in neurobiology*, *23*(2), 162-171.

Sridharan, D., Levitin, D. J., & Menon, V. (2008). A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proceedings of the National Academy of Sciences*, *105*(34), 12569–12574.

Steno, N. (1965). *Lecture on the Anatomy of the Brain*. Nyt nordisk forlag.

Su, I.-W., Wu, F.-W., Liang, K.-C., Cheng, K.-Y., Hsieh, S.-T., Sun, W.-Z., & Chou, T.-L. (2016). Pain Perception Can Be Modulated by Mindfulness Training: A Resting-State fMRI Study. *Frontiers in Human Neuroscience*, *10*. https://doi.org/10.3389/fnhum.2016.00570

Sulzer, J., Haller, S., Scharnowski, F., Weiskopf, N., Birbaumer, N., Blefari, M. L., ... & Sitaram, R. (2013). Real-time fMRI neurofeedback: progress and challenges. *Neuroimage*, *76*, 386-399.

Taren, A. A., Gianaros, P. J., Greco, C. M., Lindsay, E. K., Fairgrieve, A., Brown, K. W., Rosen, R. K., Ferris, J. L., Julson, E., & Marsland, A. L. (2015). Mindfulness meditation training alters stress-related amygdala resting state functional connectivity: A randomized controlled trial. *Social Cognitive and Affective Neuroscience*, *10*(12), 1758–1768.

Taren, A. A., Gianaros, P. J., Greco, C. M., Lindsay, E. K., Fairgrieve, A., Brown, K. W., Rosen, R. K., Ferris, J. L., Julson, E., Marsland, A. L., & Creswell, J. D. (2017). Mindfulness Meditation Training and Executive Control Network Resting State Functional Connectivity: A Randomized Controlled Trial. *Psychosomatic Medicine*, *79*(6), 674–683. https://doi.org/10.1097/PSY.0000000000000466

Taylor, V. A., Daneault, V., Grant, J., Scavone, G., Breton, E., Roffe-Vidal, S., Courtemanche, J., Lavarenne, A. S., Marrelec, G., & Benali, H. (2013). Impact of meditation training on the default mode network during a restful state. *Social Cognitive and Affective Neuroscience*, *8*(1), 4–14.

Teng, J., Massar, S. A. A., & Lim, J. (2022). Inter-relationships between changes in stress, mindfulness, and dynamic functional connectivity in response to a social stressor. *Scientific Reports*, *12*(1), 2396. https://doi.org/10.1038/s41598-022-06342-0

Tom, M. R., & Vago, D. R. (2021). Equanimity. In J. R. Peteet (Ed.), *The Virtues in Psychiatric Practice* (1st ed., pp. 61–84). Oxford University Press. https://doi.org/10.1093/med/9780197524480.003.0004

Turpyn, C. C., Chaplin, T. M., Fischer, S., Thompson, J. C., Fedota, J. R., Baer, R. A., & Martelli, A. M. (2021). Affective neural mechanisms of a parenting-focused mindfulness intervention. *Mindfulness*, *12*, 392–404.

Van Der Gucht, K., Ahmadoun, S., Melis, M., Cloe, E., Sleurs, C., Radwan, A., Blommaert, J., Takano, K., Vandenbulcke, M., Wildiers, H., Neven, P., Kuppens, P., Raes, F., Smeets, A., Sunaert, S., & Deprez, S. (2020). Effects of a mindfulness-based intervention on cancer-related cognitive impairment: Results of a randomized controlled functional magnetic resonance imaging pilot study. *Cancer*, *126*(18), 4246–4255. https://doi.org/10.1002/cncr.33074

Van Lutterveld, R., Houlihan, S. D., Pal, P., Sacchet, M. D., McFarlane-Blake, C., Patel, P. R., Sullivan, J. S., Ossadtchi, A., Druker, S., & Bauer, C. (2017). Source-space EEG neurofeedback links subjective experience with brain activity during effortless awareness meditation. *NeuroImage*, *151*, 117–127.

Vancampfort, D., Stubbs, B., Van Damme, T., Smith, L., Hallgren, M., Schuch, F., Deenik, J., Rosenbaum, S., Ashdown-Franks, G., & Mugisha, J. (2021). The efficacy of meditation-based mind-body interventions for mental disorders: A meta-review of 17 meta-analyses of randomized controlled trials. *Journal of Psychiatric Research*, *134*, 181–191.

Vogt, B. A. (2009). *Cingulate neurobiology and disease*. Oxford University Press.

Vøllestad, J., Nielsen, M. B., & Nielsen, G. H. (2012). Mindfulness-and acceptance-based interventions for anxiety disorders: A systematic review and meta-analysis. *British Journal of Clinical Psychology*, *51*(3), 239–260.

Walach, H., Buchheld, N., Buttenmüller, V., Kleinknecht, N., & Schmidt, S. (2006). Measuring mindfulness—The Freiburg Mindfulness Inventory (FMI). *Personality and Individual Differences*, *40*(8), 1543–1555. https://doi.org/10.1016/j.paid.2005.11.025

Wang, X., Xu, M., Song, Y., Li, X., Zhen, Z., Yang, Z., & Liu, J. (2014). The network property of the thalamus in the default mode network is correlated with trait mindfulness. *Neuroscience*, *278*, 291–301.

Ward, A. M., Schultz, A. P., Huijbers, W., Van Dijk, K. R., Hedden, T., & Sperling, R. A. (2014). The parahippocampal gyrus links the default-mode cortical network with the medial temporal lobe memory system. *Human Brain Mapping*, *35*(3), 1061–1073.

Wells, R. E., Yeh, G. Y., Kerr, C. E., Wolkin, J., Davis, R. B., Tan, Y., Spaeth, R., Wall, R. B., Walsh, J., Kaptchuk, T. J., Press, D., Phillips, R. S., & Kong, J. (2013). Meditation's impact on default mode network and hippocampus in mild cognitive impairment: A pilot study. *Neuroscience Letters*, *556*, 15–19. https://doi.org/10.1016/j.neulet.2013.10.001

Wen, X., Liu, Y., Yao, L., & Ding, M. (2013). Top-Down Regulation of Default Mode Activity in Spatial Visual Attention. *The Journal of Neuroscience*, *33*(15), 6444–6453. https://doi.org/10.1523/JNEUROSCI.4939-12.2013

Weng, H. Y., Lewis-Peacock, J. A., Hecht, F. M., Uncapher, M. R., Ziegler, D. A., Farb, N. A. S., Goldman, V., Skinner, S., Duncan, L. G., Chao, M. T., & Gazzaley, A. (2020). Focus on the Breath: Brain Decoding Reveals Internal States of Attention During Meditation. *Frontiers in Human Neuroscience*, *14,* 336. https://doi.org/10.3389/fnhum.2020.00336

Whitfield-Gabrieli, S., & Ford, J. M. (2012). Default mode network activity and connectivity in psychopathology. *Annual Review of Clinical Psychology*, *8*, 49–76.

Whitfield-Gabrieli, S., Thermenos, H. W., Milanovic, S., Tsuang, M. T., Faraone, S. V., McCarley, R. W., Shenton, M. E., Green, A. I., Nieto-Castanon, A., LaViolette, P., Wojcik, J., Gabrieli, J. D. E., & Seidman, L. J. (2009). Hyperactivity and hyperconnectivity of the default network in schizophrenia and in first-degree relatives of persons with schizophrenia. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(4), 1279–1284. https://doi.org/10.1073/pnas.0809141106

Williams, J. M. G., Crane, C., Barnhofer, T., Brennan, K., Duggan, D. S., Fennell, M. J., Hackmann, A., Krusche, A., Muse, K., & Von Rohr, I. R. (2014). Mindfulness-based cognitive therapy for preventing relapse in recurrent depression: A randomized dismantling trial. *Journal of Consulting and Clinical Psychology*, *82*(2), 275.

Xiong, J., Parson, L. M., Pu, Y., Gao, J. H., & Fox, P. T. (1998). Improved inter-regional connectivity mapping by use of covariance analysis within rest condition. *Proceedings of the 6th ISMRM*, 1480.

Xiong, J., Parsons, L. M., Gao, J.-H., & Fox, P. T. (1999). Interregional connectivity to primary motor cortex revealed using MRI resting state images. *Human Brain Mapping*, *8*(2-3), 151–156.

Yang, C.-C., Barrós-Loscertales, A., Li, M., Pinazo, D., Borchardt, V., Ávila, C., & Walter, M. (2019). Alterations in brain structure and amplitude of low-frequency after 8 weeks of mindfulness meditation training in meditation-naïve subjects. *Scientific Reports*, *9*(1), 1–10.

Yang, C.-C., Barrós-Loscertales, A., Pinazo, D., Ventura-Campos, N., Borchardt, V., Bustamante, J.-C., Rodríguez-Pujadas, A., Fuentes-Claramonte, P., Balaguer, R., Ávila, C., & Walter, M. (2016). State and Training Effects of Mindfulness Meditation on Brain Networks Reflect Neuronal Mechanisms of Its Antidepressant Effect. *Neural Plasticity*, *2016*, 1–14. https://doi.org/10.1155/2016/9504642

Young, K. S., van der Velden, A. M., Craske, M. G., Pallesen, K. J., Fjorback, L., Roepstorff, A., & Parsons, C. E. (2018). The impact of mindfulness-based interventions on brain activity: A systematic review of functional magnetic resonance imaging studies. *Neuroscience & Biobehavioral Reviews*, *84*, 424–433.

Zhang, D., Lee, E. K., Mak, E. C., Ho, C. Y., & Wong, S. Y. (2021). Mindfulness-based interventions: An overall review. *British Medical Bulletin*, *138*(1), 41–57.

Zhang, J., Kucyi, A., Raya, J., Nielsen, A. N., Nomi, J. S., Damoiseaux, J. S., Greene, D. J., Horovitz, S. G., Uddin, L. Q., & Whitfield-Gabrieli, S. (2021). What have we really learned from functional connectivity in clinical populations? *NeuroImage*, *242*, 118466.

Zhang, J., Raya, J., Morfini, F., Urban, Z., Pagliaccio, D., Yendiki, A., Auerbach, R. P., Bauer, C. C., & Whitfield-Gabrieli, S. (2023). Reducing default mode network connectivity with mindfulness-based fMRI neurofeedback: A pilot study among adolescents with affective disorder history. *Molecular Psychiatry*, 1–9.

Zhou, L., Pu, W., Wang, J., Liu, H., Wu, G., Liu, C., Mwansisya, T. E., Tao, H., Chen, X., & Huang, X. (2016). Inefficient DMN suppression in schizophrenia patients with impaired cognitive function but not patients with preserved cognitive function. *Scientific Reports*, *6*(1), 21657.

Zou, Q. H., Zhu, C. Z., Yang, Y., Zuo, X. N., Long, X. Y., Cao, Q. J., ... & Zang, Y. F. (2008). An improved approach to detection of amplitude of low-frequency fluctuation (ALFF) for resting-state fMRI: fractional ALFF. *Journal of neuroscience methods*, *172*(1), 137-141.

## Box 1

Linking State and Trait Mindfulness through Dynamic Functional Connectivity

**Box 1: Linking State and Trait Mindfulness through Dynamic Functional Connectivity**

- ◊ There are two viewpoints on what resting-state FC actually represents (Kucyi, 2018). On the one hand, functional connectivity may be similar to anatomical connectivity in that it constrains and undergirds cognition. The correlations between brain areas over the course of a scan may not necessarily be related to cognitive processes in the moment. In this view, functional connectivity is ‘intrinsic’. On the other hand, functional connectivity may actually support states of awareness, it may be ‘stateful’. Thus there may be distinct signatures of mindfulness - a true intrinsic, ‘trait’ way the brain is organized, and a ‘stateful’ way the brain is engaged by mindfulness practice.
- ◊ The best method we have to explore these possibilities is dynamic functional connectivity (DFC), which models the brain as going through nonstationary processes throughout an fMRI scan. In the studies examining mindfulness and DFC, investigators use a method called clustering (Allen et al., 2014). Connectivity matrices (correlations between sets of regions or nodes) are calculated in time windows, and they are clustered into centrotypes, or most representative matrices, also called brain states. Each time window can then be classified as belonging to a brain state. One can then examine a suite of dynamic measures including how long a participant has spent in a given state throughout the course of the scan, how many transitions are made between states, etc. (**Figure 2)**.
- ◊ In one study, researchers examined DFC in 38 college-age participants while they performed a 9-minute breathing exercise (Mooneyham et al., 2017). DFC was assessed between *a priori* seeds in the DMN, FPN, and SN. The authors found one state (one pattern of connectivity) where the DMN was anticorrelated with the FPN and SN. More mindful individuals spent more time in this state (‘dwell time’) during the scan. A mindfulness intervention increased dwell time in this state. Interestingly, those individuals who showed larger changes in trait mindfulness due to the mindfulness intervention showed the largest increases in dwell time. The authors interpreted this state as having to do with focused attention, and contrasted it with another, mind-wandering, state. Other studies of DFC have also found trait mindfulness increases time in states where the DMN and other networks are anticorrelated (Lim et al., 2018; Marusak et al., 2018; in response to stress: Teng et al., 2022).
- ◊ This literature provides a useful link between trait mindfulness and state mindfulness. Individuals with higher trait mindfulness may spend more time in a state of focused, present-centered attention. Mindfulness training may consist of deepening these states of mindfulness and making them more frequent, thus leading to increases in trait mindfulness.

**Table 1**

Overview of mindfulness interventions effects on resting-state fMRI studies.

| **Resting-state studies** | **Mindfulness intervention/ Control** | **Number of participants** | **Method** | **Resting-state findings for Mindfulness > Control** | **Citations** |
|---|---|---|---|---|---|
| **TYPE: Static FC** | | | | | |
| Bauer et al., 2020 | 8-week mindfulness/ coding | 31 (sixth-graders) | Seed-based | DMN-CEN ⇓ | 29 |
| Bremer et al., 2022**** | 1-month mindfulness/ health training | 46 | Seed-based/ ICA | DMN-SN ⇑ SN-CEN ⇑ | 4 |
| Chumachenko et al., 2021 | MBSR/ healthy living | 52 | Seed-based/ ICA | VMPFC-Amygdala ⇑ | 9 |
| Creswell et al., 2016 | 3-day intensive retreat/ relaxation training* | 35 (unemployed) | Seed-based | DMN-CEN ⇑ | 311 |
| Gan et al., 2022*** | MBSR/ relaxation | 32 | Seed-based | Within-SN ⇑ | 1 |
| Kilpatrick et al., 2011 | MBSR/ waitlist control | 32 (women) | ICA | Within-auditory, within-visual ⇑ between auditory-visual⇓, dmPFC-pgACC ⇑, DMN-SN ⇓, | 440 |
| King et al., 2016 | 16-week mindfulness-based exposure therapy/ present-centered group therapy | 23 (male veterans) | Seed-based | DMN-CEN ⇑ | 196 |
| Kral et al., 2019 | MBSR/HEP/waitlist | 140 | Seed-based | DMN-CEN ⇑ | 49 |
| Kwak et al., 2019 | 4-day retreat/ relaxation | 47 | Seed-based | DMN-SN ⇑ | 34 |
| Lifshitz et al., 2019 | 2-week mindfulness/ relaxation | 31 | Seed-based | Within CEN ⇓ | 10 |
| Shao et al., 2016 | Mindfulness/ relaxation | 40 (Elderly) | Seed-based/ DCM | DMN- Brainstem (Pons) ⇑ DMN-Somatomotor ⇓ | 36 |

| | | | | | |
|---|---|---|---|---|---|
| Su et al., 2016 | 6-week intervention, NO CONTROL | 34 | Seed-based | Within-SN ⇑ (in chronic pain cohort) | 26 |
| Taren et al., 2015 | 3-day intensive retreat/ relaxation training* | 130 | Seed-based | Right amygdala- sgACC connectivity ⇓ | 202 |
| Taren et al., 2017 | 3-day intensive retreat/ relaxation training* | 35 | Seed-based | Within-CEN (DLPFC-DAN/ DLPFC-VAN) ⇑ | 154 |
| Turpyn et al., 2021 | Mindful parenting/ parent education | 20 (mothers of adolescents) | Seed-based | DMN-SN ⇓ Right insula – left middle temporal cortex ⇓ SN-Somatomotor ⇓ | 5 |
| Van Der Gucht et al., 2020 | MBSR/ waitlist | 25 (cancer survivors with cognitive impairment) | Seed-based | SN – DAN ⇑ | 27 |
| Wells et al., 2013 | MBSR/ waitlist control | 13 (cognitive impairment) | Seed-based | Within-DMN ⇑ | 236 |
| Yang et al., 2016 | MBSR, NO CONTROL** | 13 | Seed-based | DMN (precuneus/PCC)- SN (pgACC) ⇓ DMN (PCC)- SN (dACC) ⇑ SN-CEN | 83 |
| **TYPE: Dynamic FC** | | | | | |
| Bremer et al., 2022**** | 1-month mindfulness/ health training | 46 | Clustering | DMN-SN ⇑ within a specific state. | 4 |
| Mooneyham et al., 2017 | 6-week intervention/ waitlist control | 38 | Clustering | Dwell time greater in state with correlations SN-CEN. anticorrelations DMN-SN, DMN-CEN | |
| **TYPE: Other** | | | | | |
| Gan et al., 2022*** | MBSR/ relaxation | 32 | ALFF | ALFF in SN⇓ | 1 |
| Yang et al., 2019 | MBSR, NO CONTROL ** | 14 | ALFF | ALFF in DMN⇓ | 55 |

*Note.* MBSR: Mindfulness-based stress reduction. HEP: Health Enhancement Program, ALFF: amplitude of low-frequency fluctuations. DMN: default-mode network. CEN: central executive network. SN: salience network. DAN: dorsal attention network. VAN:ventral attention network. DFC: dynamic functional connectivity. * To the best of our knowledge, these studies followed the same procedures . ** To the best of our knowledge, these studies followed the same procedures. *** Gan et al. (2022), used both static FC and ALFF methods on same sample, **** Bremer et al. (2022), used both static FC and dynamic FC on the same sample.

**Table 2**

Overview of resting-state fMRI studies on trait mindfulness.

| Resting-state studies | Trait mindfulness measure | Number of participants | Resting-state findings for greater trait mindfulness |
|---|---|---|---|
| **TYPE: Static FC** | | | |
| Shaurya Prakash et al., 2013 | MAAS | 25 (Elderly) | Within-DMN ⇑ |
| Wang et al., 2014 | MAAS | 245 | Within-DMN ⇓ (Thalamus seed) |
| Doll et al., 2015 | MAAS | 26 | Within-DMN ⇓ |
| | FMI | 26 | DMN-SN ⇓ |
| Bilevicius et al., 2018 | MAAS | 32 | Within-SN ⇑ Within-FPN ⇑ Within-DMN ⇓ DMN-SN ⇓ DMN-FPN ⇓ |
| Parkinson et al., 2019 | FFMQ | 28 | DMN-SN⇑ , DMN-FPN⇓, within-DMN⇓, within-SN⇑ (observing), within-DMN ⇑ (non-judging), ATN-DMN ⇑ (non-judging) |
| Harrison et al., 2019 | FFMQ | 40 | Within-DMN ⇓, DMN-SMN ⇑ |
| Hunt et al., 2022 | FFMQ | 98 migraine patients , 36 healthy controls | No relationship with within-DMN, post-hoc: DMN-cerebellum ⇑ vmPFC-DMN ⇑ (non-judging)** and greater DMN-SN⇑ (non-judging)** |
| **TYPE: Dynamic FC** | | | |
| Mooneyham et al., 2017 | MAAS | 38 | Dwell time greater in state with correlations SN-FPN. anticorrelations DMN-SN, DMN-FPN |
| Lim et al., 2018 | FFMQ*** | 39 | Dynamic: dwell time greater in state with DMN-SN anticorrelations, high within-DMN, within-SN correlations. Static: DAN-DMN ⇓, VAN-DMN ⇓. |
| Marusak et al., 2018 | CAMM | 42 (Children) | Dwell time lesser in state with high correlations DMN-FPN, FPN-FPN, anticorrelations FPN-SN, DMN-SN |
| Teng et al., 2022 | FFMQ | 40 | No correlation with dwell time* in state with high within-DMN, anticorrelations in DMN-FPN |
| **TYPE: Other** | | | |
| Kong et al., 2016 | MAAS | 270 | ReHo ⇑ OFC, PHG, Insula<br>ReHo ⇓ IFG |
| Li et al., 2022 | FFMQ | 89 | ALFF negatively correlates in PCG (non-reactivity), negatively correlates with PMC |

*Note*. FFMQ: Five Facet Mindfulness Questionnaire, MAAS: Mindfulness Attention Awareness Scale, CAMM: Child and Adolescent Mindfulness Measure, FMI: Frieburg Mindfulness Inventory. FC: functional connectivity, DMN: Default Mode Network, SN: Salience Network, FPN: Frontoparietal network, ATN: attentional network including dorsal and ventral components, SMN: Somatomotor network, DAN: dorsal attention network, VAN: ventral attention network, ReHo: regional homogeneity, IFG: inferior frontal gyrus, OFC: orbitofrontal cortex, PHG: parahippocampal gyrus, ALFF: amplitude of low frequency fluctuations, PCG: posterior cingulate gyrus, PMC: premotor cortex, vmPFC: ventromedial prefrontal cortex. Results for Doll et al., 2015 are separated by mindfulness scale (samples are overlapping). * After a stressor, more mindful individuals exhibited more dwell time in state. ** Only in patient sample. *** Researchers also found comparable results for objective breath-counting measure.

**Table 3**

Glossary

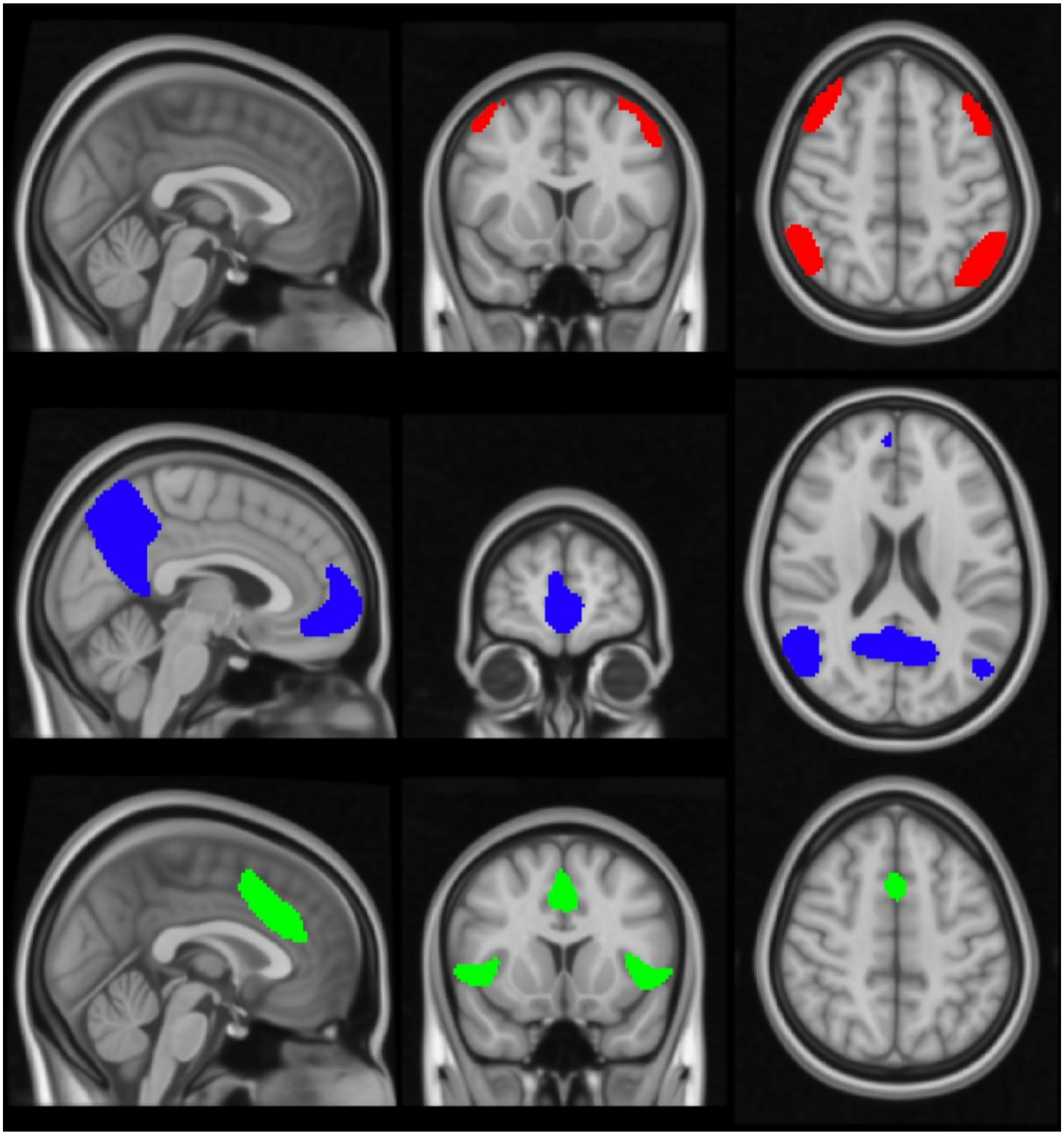
| | |
|---|---|
| ACC | Anterior Cingulate Cortex - A brain region involved in various cognitive and emotional processes, including decision-making, conflict monitoring, and emotion regulation (Vogt, 2009). |
| ALFF | Amplitude of Low-Frequency Fluctuations - A metric used in resting-state fMRI to measure the amplitude of spontaneous low-frequency brain activity in brain regions (Zou et al., 2008). |
| Amygdala | A small, almond-shaped structure in the brain's temporal lobe that plays a crucial role in processing emotional information, particularly fear and anger. It is also involved in mood disorders such as MDD and bipolar disorder (Drevets et al., 2008). |
| Anticorrelations | Negative correlations between brain regions - When the signal timecourses of two brain regions are inversely related to each other during certain tasks or resting state, it is referred to as an anticorrelation (Fox et al., 2005). |
| BOLD | Blood Oxygen Level Dependent - A contrast mechanism used in fMRI that relies on changes in blood oxygenation to indirectly measure neural activity (Ogawa et al., 1990). |
| Connectomics | Study of brain connectivity - Connectomics is a field of neuroscience that focuses on understanding the brain's structural and functional connectivity patterns and their relation to brain function and behavior (Sporns, 2013). |
| DFC | Dynamic Functional Connectivity – Temporally varying functional connectivity between brain regions over time (Hutchison et al., 2013). |
| dmPFC | Dorsomedial Prefrontal Cortex - A region of the brain's prefrontal cortex involved in cognitive control, social cognition, and emotional regulation (Bzdok et al., 2013). |
| DLPFC | Dorsolateral Prefrontal Cortex - A region of the brain's prefrontal cortex that is involved in working memory, cognitive flexibility, and decision-making (Scharnowski et al., 2015). |
| DMN | Default Mode Network - A network of brain regions that are active during rest and self-referential mental processes, but show decreased activity during externally focused tasks (Raichle et al.,2001). |

| | |
|---|---|
| fMRI | Functional Magnetic Resonance Imaging - A neuroimaging technique that measures brain activity by detecting changes in blood flow and oxygenation, providing insights into functional brain organization (Logothetis & Pfeuffer, 2004). |
| FC | Functional Connectivity - The degree of temporal correlation or synchronization between brain regions, indicating their functional interactions and integration (Friston et al., 1995). |
| FFMQ | Five Facet Mindfulness Questionnaire - A self-report measure assessing various aspects of mindfulness, including observing, describing, acting with awareness, non-judging, and non-reacting (Baer et al., 2006). |
| FPN/CEN | Frontoparietal Network/Central Executive Network - A network of brain regions involved in cognitive control, attention, and executive functions (Cole et al., 2013). |
| GroupICA | Group Independent Component Analysis - A technique used in fMRI analysis to identify common spatial patterns of brain activity across participants in group studies (Calhoun et al., 2001). |
| Hub | A node in a network that has a high number of connections to other nodes, serving as a central point of communication and information flow (Sporns, 2011) |
| ICA | Independent Component Analysis - A statistical method used to decompose complex signals, such as fMRI data, into independent components that represent different sources of neural activity (Hyvärinen & Oja, 2000). |
| insSN | Insula Salience Network - A network of brain regions involved in processing salient stimuli and regulating interoceptive and emotional responses (Menon & Uddin, 2010). |
| IPL | Inferior Parietal Lobe - A region of the brain’s parietal cortex involved in various cognitive functions, including attention, spatial awareness, and numerical processing (Cabeza et al., 2008). |
| MAAS | Mindfulness Attention Awareness Scale - A self-report measure assessing an individual's trait mindfulness through questions about attentional lapses in their daily life (Brown & Ryan, 2003). |
| mPFC | Medial Prefrontal Cortex - A region of the brain’s prefrontal cortex involved in self-referential processing, social cognition, and emotional regulation (Amodio & Frith, 2006). |
| PCC | Posterior Cingulate Cortex - A region of the brain’s cingulate cortex involved in various cognitive processes, including memory, self-referential processing, and the default mode network (Buckner et al., 2008). |
| rsFC | Resting State Functional Connectivity - Functional connectivity measured during rest, when participants are not engaged in specific cognitive tasks, providing insights into the brain's intrinsic functional organization (Biswal et al., 1995). |
| ROI | Region of Interest - A specific brain region or area that is selected for analysis or measurement due to its relevance to the research question (Friston et al., 1994). |
| rt-fMRI: | Real-Time fMRI Neurofeedback - A technique that provides real-time feedback of an individual's brain activity during fMRI scanning, allowing them to modulate brain responses through self-regulation (Sulzer et al., 2013). |

| | |
|---|---|
| sgACC | Subgenual Anterior Cingulate Cortex - A region of the brain's prefrontal cortex that has been implicated in the regulation of emotional behavior and stress response. It is also involved in mood disorders such as major depressive disorder (MDD) and bipolar disorder (Drevets et al., 2008; Drevets & Raichle, 1998). |
| SLFs | Spontaneous Low-Frequency Signal Fluctuations - The fluctuations in the BOLD signal occurring at low frequencies, often studied to investigate intrinsic brain activity and connectivity (Biswal et al., 1995). |
| SN | Salience Network - Involved in detecting and filtering salient stimuli A network of brain regions involved in detecting and directing attention to salient or relevant stimuli in the environment (Seeley et al., 2007). |
| Somatosensory Network | A network of brain regions that are involved in processing sensory information from the body, including touch, temperature, and pain. It includes the primary somatosensory cortex, secondary somatosensory cortex, and insula (Goswami et al., 2011). |
| Task-Negative | Brain regions that are active during rest and less active during task performance - Brain regions that show decreased activity during task performance compared to rest, often associated with the Default Mode Network (Raichle et al., 2001). |
| Task-Positive | Brain regions that are active during task performance and less active during rest - Brain regions that show increased activity during task performance compared to rest, often associated with the Central Executive Network (Fox et al., 2005) |
| Thalamus | A structure in the brain that acts as a relay station for sensory information, including pain, touch, and temperature. It is also involved in regulating consciousness, sleep, and alertness (Drevets et al., 2008). |
| TR | Time of Repetition - The time interval between successive volumes acquired during an fMRI scan (Bandettini et al., 1993). |
| Voxels | Short for "volumetric pixels," voxels are three-dimensional units used to represent a specific volume of brain tissue in neuroimaging, including techniques like fMRI and MRI (Ogawa et al., 1990). |

**Figure 1**

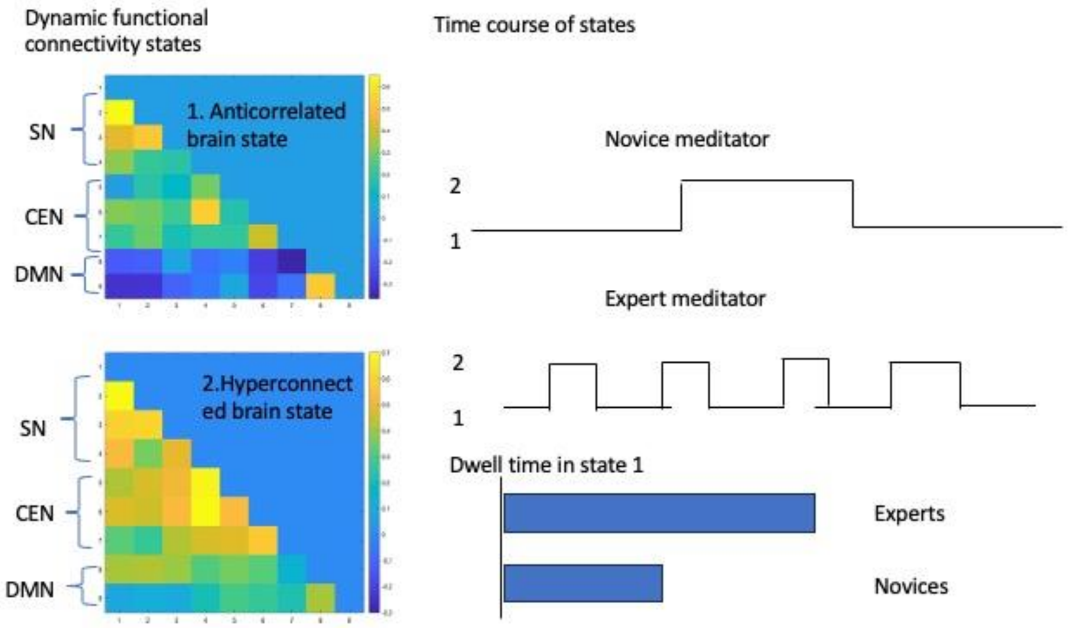
Triple networks



*Note:* Central executive network, in red; Default-mode network, in blue; Salience network, in green.

**Figure 2**

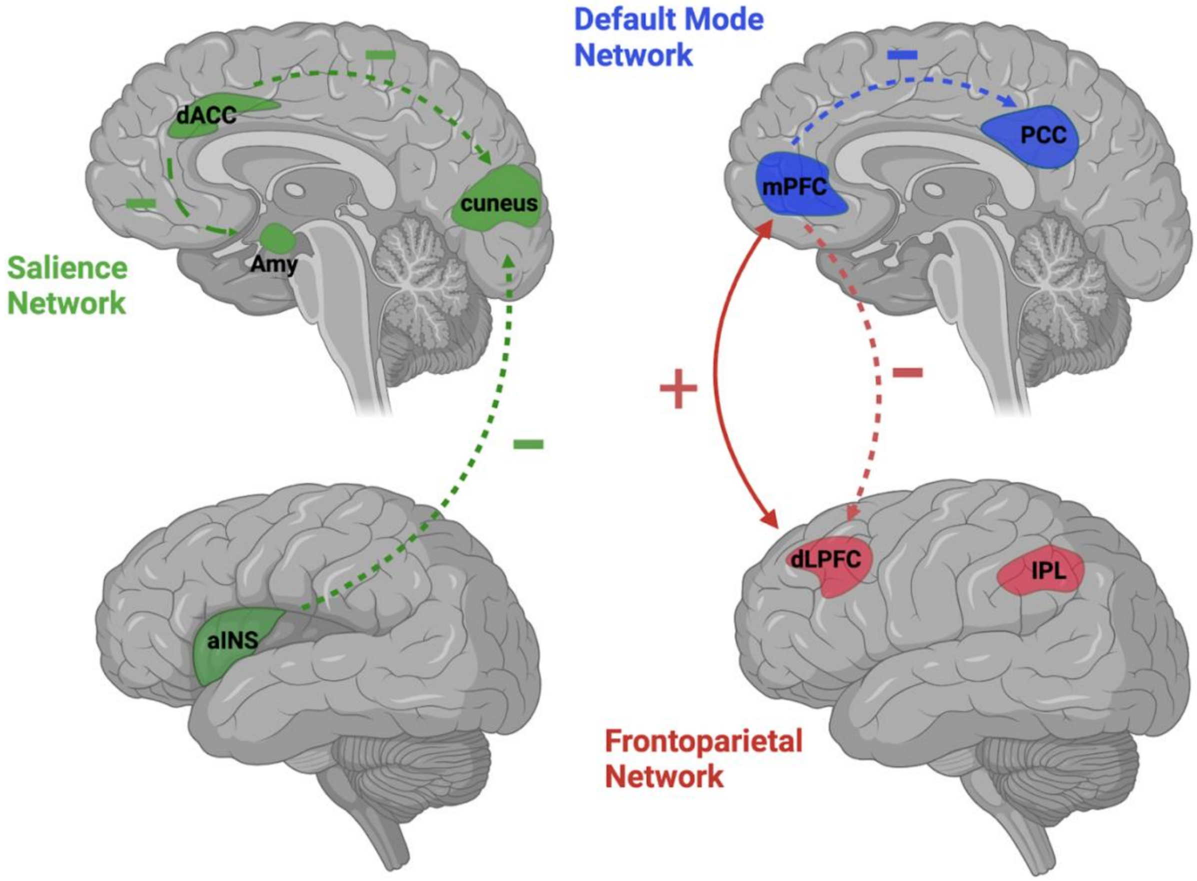
Dynamic functional connectivity states (unpublished data), and potential outcomes



*Note.* Dynamic functional connectivity states (unpublished data), and potential outcomes. On left, states derived from clustering connectivity between regions in the triple networks. There may be an anticorrelated, sustained attention state and a hyperconnected, mind-wandering state. One possible outcome is that expert meditators may experience more fluctuations between states, due to more flexibility at rest. Another possible outcome is that dwell-time in the sustained attention state may be greater in expert meditators.

**Figure 3**

Visualization of Brain Networks



*Note.* Visual rendering of the Default Mode Network (DMN; blue), Frontoparietal Network (FPN; red) and Salience Network (SN; green) and their functional connectivity changes mediated by mindfulness. Current literature supports the possibility of : (a) Reduced within-DMN connectivity across intervention designs, trait designs, and long-term meditator designs (blue dotted arrow). (b) Interventions and active meditation may increase DMN-FPN connectivity (red full arrow). (c) Trait mindfulness studies suggest that DMN-FPN may actually be more anticorrelated in more mindful individuals (red dotted arrow). (d) Decreased connectivity between rostral anterior cingulate cortex region and amygdala (green dotted arrow). Abbreviations: dACC = dorsal anterior cingulate cortex, mPFC = medial prefrontal cortex, PCC = posterior cingulate cortex, aINS = anterior insula, dlPFC = dorsal prefrontal cortex, IPL = inferior parietal lobule, Amy = Amygdala. Adapted from Sezer et al. (2022), with permission.