Disrupting The Resting State: Meta-Analytic Evidence That Mindfulness Training Alters Default Mode Network Connectivity

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Research Article

Keywords: mindfulness, connectivity, Network,

Posted Date: January 6th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1189676/v1>

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Abstract

This meta-analysis sought to expand upon neurobiological models of mindfulness through investigation of inherent brain network connectivity outcomes, indexed via resting state functional connectivity (rsFC). We conducted a systematic review and meta-analysis of rsFC as an outcome of mindfulness training (MT) relative to structurally-equivalent programs, with the hypothesis that that MT would increase cross-network connectivity between nodes of the Default Mode Network (DMN), Salience Network (SN), and Frontoparietal Control Network (FPCN) as a mechanism of internally-oriented attentional control. Texts were identified from the databases: MEDLINE/PubMed, ERIC, PSYCINFO, ProQuest, Scopus, and Web of Sciences; and were screened for inclusion based on experimental/quasi-experimental trial design and use of standardized mindfulness-based interventions. RsFC effects were extracted from twelve studies (mindfulness $n = 226$; control $n = 204$). Voxel-based meta-analysis revealed significantly greater rsFC (MT > control) between the left middle cingulate (*Hedge's* $g = .234$, $p = .0288$, $I^2 = 15.87$), located within the SN, and the posterior cingulate cortex, a focal hub of the DMN. Egger's test for publication bias was nonsignificant, bias = 2.17, $p = .162$. In support of our hypothesis, results suggest that MT targets internetwork (SN-DMN) connectivity implicated in the flexible control of internally-oriented attention.

Introduction

Human waking life contains many moments in which the mind is not engaged by external goals or tasks, but is instead absorbed in a state of stimulus-independent thought (SIT) (Christoff et al., 2004; Mason et al., 2007), commonly referred to as “mind wandering” and “resting state activity”. Experience sampling studies suggest that SIT is often self-reflective and focuses on the evaluation of past experiences and the simulation of future events (Diaz et al., 2013; Fox et al., 2015). The content and dynamics of SIT have been shown to vary considerably between individuals (Andrews-Hanna et al., 2013; Smallwood & Schooler, 2015), with important implications for mental health. While SIT appears to serve multiple adaptive functions, including self-regulation (Uchicha et al., 2015; Morawetz et al., 2016), memory consolidation (Censor et al., 2014; de Voogd et al., 2017), and problem solving (Hearne et al., 2017; Ito et al., 2017), the resting mind can paradoxically become restless in nature when thoughts are negatively-oriented, repetitive, or intrusive (Smallwood & Schooler, 2006; Nolen-Hoeksema et al. (2008) Andrews-Hanna et al., 2014). Such perseverative cognitions reinforce maladaptive coping strategies endemic to affective disorders (e.g., anxiety and depressive conditions) (Watkins, 2008; Kaplan et al., 2018; Spinhoven et al., 2019; Watkins & Roberts, 2020).

The disruption of repetitive negative thinking is notoriously challenging (Mennin & Fresco, 2013; Watkins & Roberts, 2020); however, research suggests that cognitive training in mindful awareness may alter the resting mind so as to function more adaptively (Hasenkamp & Barsalou, 2012; Vago & Zeidan, 2016). The effects of mindfulness training for the treatment of affective disorders and concomitant rumination are well-documented (Piet et al., 2011; Vøllestad et al., 2012; Gu et al., 2015; Perestelo-Perez et al., 2017); however, the mechanistic involvement of resting state activity is less well-understood. Prevailing theory posits that mindfulness training may alter such activity via attentional mechanisms, ostensibly reflected in the reorganization of neural circuitry (Hölzel et al., 2011; Tang et al., 2015; Vago & Zeidan, 2016). Accordingly, recent research has begun to investigate resting state neural circuitry as an outcome of mindfulness training (e.g., Kilpatrick et al., 2011; Kral et al., 2019) and as a characteristic of dispositional mindfulness (e.g., Doll et al., 2015; Bilevicius et al., 2018; Harrison et al., 2019; Parkinson et al., 2019). Such studies support the involvement of candidate interacting brain networks—including the default mode network (DMN), salience network (SN), and the frontoparietal control network (FPCN)—through which mindfulness may facilitate the flexible allocation of attentional resources between introspective and perceptual processes (Dixon et al., 2018). However, there remains little consensus about how mindfulness alters functional connectivity within and between these networks. The current meta-analysis sought to update brain-based models of mindfulness by comprehensively examining mindfulness-driven resting state functional connectivity (rsFC) outcomes.

The Neurocognitive Features of Stimulus Independent Thought (SIT)

When measured as functional connectivity, changes in neural circuitry reflect strengthened or weakened coordination between regions and, at a larger scale, between networks of interest (Van Dijk et al., 2010; Buckner et al., 2013). Analogous to the spontaneous flow of thought characteristic of resting states, the brain at rest spontaneously emits blood oxygen level dependent (BOLD) fluctuations that self-organize into cohesive neural networks (Raichle et al., 2001; Fox & Raichle, 2007) that are commonly termed ‘resting-state’ or ‘intrinsic’ functional networks (Snyder & Raichle, 2012). Although there is little consistency in the taxonomy of intrinsic functional networks (for review see Uddin et al., 2019), it is generally accepted that a minimum of 10 networks are observable during the resting state (Damoiseaux et al., 2006).

Among recognized large-scale networks, the DMN, SN, and FPCN have been frequently implicated in explanatory frameworks of SIT. The DMN has received the most attention historically for its role in internally-directed mentation (Andrews-Hanna et al., 2014; Raichle, 2015). Indeed, prevailing evidence suggests that the primary function of the DMN may be the generation and maintenance of internal mental processes (Andrews-Hanna et al., 2010a; Axelrod et al., 2017). The DMN may be further parcelled into three subnetworks, the midline-located core DMN, the medial temporal lobe subsystem (DMN-MTL), and the dorsomedial prefrontal cortex subsystem (DMN-dmPFC) (Andrews-Hanna et al., 2010b). While each subnetwork supports different functions of internally oriented mentation, the core DMN—encompassing the posterior cingulate cortex (PCC) and ventromedial prefrontal cortex (vmPFC)—is most robustly associated with self-referential thought (Legrand & Ruby, 2009; Andrews-Hanna et al., 2010b; van Buuren et al., 2010; Denny et al., 2012). Hyperconnectivity within the core DMN has been reliably observed in psychopathologies characterized by self-focused perseverative cognition (i.e., depression) (Kaiser et al., 2015; Coutinho et al., 2016; Lois & Wessa, 2016); however, the role of the DMN in maladaptive SIT is likely more complex. In support of this viewpoint, neural models of SIT suggest that the regulation (or dysregulation) of internal mental states relies on inter-network coordination between the DMN and networks implicated in attention, namely the SN and FPCN (Sridharan et al., 2008; Leech & Sharp, 2014; Dixon et al., 2018).

According to the dynamic framework of mind-wandering (Christoff et al., 2016), internal experiences—maintained by the DMN—may be deliberately or automatically constrained via coordination with the FPCN and SN, respectively. The FPCN, characterized by dorsolateral PFC and anterior inferior parietal structures (Uddin et al., 2019), is well-known for its integral role in cognitive control processes (Zanto & Gazzaley, 2013). Studies combining experience sampling with neuroimaging suggest that the FPCN flexibly couples with the DMN to deliberately regulate internal mentation (Cole et al., 2013), and that such coordination is used to inhibit internal thought when external attention is required (Spreng et al., 2010; Gao & Lin, 2012).

In contrast, the SN has been theorized to support automatic constraints on internal experiences through cognitively efficient cross-network signaling (Christoff et al., 2016). Key nodes of the SN include the midcingulate cortex (MCC) [also known as the dorsal anterior cingulate cortex (dACC) (Allman et al., 2001)] and anterior insula (Uddin et al., 2019), which jointly operate within a cortico-striato-thalamo-cortical loop to detect motivationally important stimuli, either internal or external (Peters et al., 2016). Through its extensive connectivity with the DMN and FPCN, the SN facilitates “set-shifting” by automatically and flexibly directing attention to and from internal and external cues (Seeley et al., 2007; Sridharan et al., 2008). Interestingly, SN engagement has also been suggested as a putative mechanism of perseverative cognition (Andrews-Hanna et al., 2019). According to this viewpoint, aberrant SN connectivity exacerbates interoceptive awareness of unpleasant sensations, and due to the high motivational value of ruminative thoughts, draws attentional resources to internally-directed mentation (Andrews-Hanna et al., 2019). While this theory is indirectly supported by evidence of SN hyperconnectivity in high-rumination individuals (Kühn et al., 2012; Kühn et al., 2014), it fails to explain why therapies aiming to enhance awareness of internal experiences (i.e., mindfulness) would ameliorate ruminative thought. Thus further research is warranted to elucidate how cognitive training, like mindfulness, alters the dynamics of internal experiences at both a subjective and neurobiological level.

Multi-method investigations suggest that variability in functional connectivity within and between networks likely reflects the content and dynamics of internal mentation (Doucet et al., 2012; Diaz et al., 2013; Marchetti et al., 2015), and resting state functional connectivity (rsFC) has been associated with individual differences in symptoms of anxiety (Liao et al., 2010), depression (Kaiser et al., 2015; Drysdale et al., 2017), and trait rumination (Rosenbaum et al., 2017; Satyshur et al., 2018). Thus neurocircuitry reorganization via rsFC has been suggested as a key mechanism of treatment for psychopathologies featuring repetitive negative thought (Broyd et al., 2009; Dichter et al., 2015; Klumpp & Fitzgerald, 2018; Xu et al., 2019; Feurer et al., 2021). Although the research is nascent, there is initial evidence that mindfulness training may improve regulation of mental states, and that rsFC indices may be used to better understand the mechanisms through which mindfulness extends its therapeutic effects (e.g., Creswell et al., 2016).

Mechanisms of Mindfulness: Theory and Empirical Support

Mindfulness, commonly defined as the act of attending to present-moment thoughts, emotions, and sensations without judgment or appraisal (Brown & Ryan, 2003), is relatively unique as a treatment of maladaptive SIT. Unlike popular cognitive behavioral therapies (CBTs), which enable the individual to challenge dysfunctional thoughts (Beck, 2012), mindfulness instead targets one's relationship to such thoughts (Kabat-Zinn, 1994; Segal et al., 2018). This non-judgmental stance towards internal experiences may be promoted through a combination of neurocognitive mechanisms (for review see Hölzel et al. 2011; Vago & Silbersweig, 2012; Tang et al., 2015; Vago & Zeidan, 2016; Fox et al., 2014; Fox & Cahn, 2018; Young et al., 2018). Mounting evidence indicates that mindfulness practice enhances *attentional control*, which may potentially support the deliberate constraint of maladaptive SIT (Andrews-Hanna et al., 2020). Foundational to the practice of mindfulness is the development of attentional control through a meditative technique called Focused Attention (FA). FA meditation trains the practitioner to focus on and maintain attention to a neutral sensory object (e.g., the breath), and direct attention back

to that object when the mind begins to wander (Lutz et al., 2008). This recursive process of shifting and sustaining attention has previously been linked to enhanced functional connectivity within the FPCN of experienced meditators (Hasenkamp & Barsalou, 2012), suggesting that FA improves top-down cognitive control needed to disengage from distracting thoughts and emotions.

Alternative models of mindfulness posit that mindfulness may *indirectly* regulate SIT by promoting *awareness* of internal experiences (Vago & Silbersweig, 2012). According to this framework, the sustained concentration conferred by mindfulness facilitates awareness (or mindful meta-awareness), defined as the capacity to observe one's mental patterns with a sense of equanimity and psychological distance (Lutz et al., 2008; Dunne et al., 2019). This internal awareness thereby supports recognition of thoughts and feelings as discrete mental states, and in turn, improves flexible, adaptive responding (Lutz et al., 2008). The cultivation of mindful awareness has been theoretically attributed to enhanced functional cohesion of networks linked to self-awareness (e.g., default mode network) and attention monitoring (e.g., salience networks) (Hasenkamp & Barsalou, 2012; Tang et al., 2015). However, support for this neural model draws largely from cross-sectional research (e.g., Brewer et al., 2011; Hasenkamp & Barsalou, 2012; Farb et al., 2013), as well as correlational evidence (Doll et al., 2015; Bilevicius et al., 2018; Harrison et al., 2019; Parkinson et al., 2019). Moreover, this neural model of mindful awareness does not fully account for the role of *non-judgment, or acceptance*, which may operate in tandem with awareness to reduce "experiential fusion" with one's thoughts (Bernstein et al., 2019; King & Fresco, 2019). It has been speculated that mindfulness may dampen experiential fusion through DMN downregulation (King & Fresco, 2019; Vago & Silbersweig, 2012); however, it is unclear how neural substrates of attention and awareness may mediate such effects.

Building on previous models of mindfulness meditation (Hölzel et al. 2011, Vago & Silbersweig, 2012; Tang et al., 2015; Vago & Zeidan, 2016), it is plausible that mindfulness training (MT) alters the resting state via reorganization of neural circuitry (i.e., intrinsic functional connectivity). Specifically, we posit that focused attention training recruits the FPCN, implicated in cognitive control and executive function. Given its documented role as a 'hub' of functional connectivity (Cole et al., 2013), the FPCN may plausibly facilitate functional connections between other resting state networks—particularly between networks related to mind-wandering (i.e., default mode network) and internal awareness (i.e., salience network)—thus enabling the flexible regulation of mental states (Vago & Silbersweig, 2012). Coupled with improvements in executive functioning, such functional coordination between DMN and SN may likewise support meta-awareness skills needed to identify and disengage from maladaptive cognitive patterns. To extend this theoretical framework, the present study posed the question: Does mindfulness training facilitate flexible switching between DMN, salience, and FPCN during rest?

Present Study

The aim of this study was to determine if mindfulness training modifies intrinsic functional connectivity (IFC) observed during resting states. Specifically, this study sought to examine connectivity within and between the frontoparietal control network (FPCN), the default mode network (DMN), and salience network (SN). To date, several studies have investigated the impact of mindfulness training on resting state functional connectivity (rsFC) using controlled, experimental designs (Brewer et al., 2011; Froeliger et al., 2012; Creswell et al., 2016; King et al., 2016). Although insightful, such studies typically suffer from low statistical power, a limitation endemic to research relying on high-cost neuroimaging modalities such as fMRI. Addressing such concerns, meta-analytic approaches may be used to pool information from well-controlled studies while modeling convergence of effects across pooled samples. Thus, we conducted a systematic review and meta-analysis of rsFC outcomes of mindfulness training relative to structurally-equivalent programs (i.e., active controls). To test the neuroplastic changes associated with mindfulness skills—namely, executive functioning and meta-awareness—we hypothesized that 1) mindfulness training would enhance rsFC between the FPCN and DMN as an indicator of enhanced cognitive control; and 2) mindfulness training would enhance rsFC between the DMN and SN, reflective of meta-awareness.

Results

Study characteristics and participant demographics are displayed in Table 1. Overall, studies used standardized mindfulness-based interventions and structurally equivalent control interventions ranging from 3 days to 8 weeks in length. Study samples varied in terms of age ($M = 45.80$; $SD = 13.15$) and clinical characteristics with the majority of studies recruiting healthy adults (see Table 1). The majority of individuals from the pooled sample identified as female ($n = 286$, 62.72%) followed by male ($n = 170$, 37.28%). No studies reported data from trans or non-binary participants. Of the 12 included studies, only 5 reported racial/ethnic demographic information. From this subsample of 152 participants, 100 (65.79%) identified as white, 31 (20.39%) as Black/African American, 12 (7.89%) as Mixed Race/Other, 5 as Hispanic/Latino (3.29%), 3 (1.97%) as Asian, and 1 as Southeast Asian (0.66%).

Seed regions were pooled according to standardized resting state network location. This process demonstrated that eligible studies used seed regions from four networks, the default mode network (DMN; $n = 11$), the midcingulo-insular network (M-CIN; $n = 7$), the dorsal attention network (DAN; $n = 1$), and the frontoparietal control network (FPCN; $n = 2$) (see Supplementary Table S1).

SDM meta-analysis was used to test for significant training condition effects. Meta-analysis results identified one significant cluster of 57 voxels located in the paracingulate gyri (Table 2, Figure 2), *Hedge's g* = .234, *p* = .0288, I^2 = 15.87, suggesting that mindfulness training, relative to control training programs, increased connectivity to bilateral median cingulate regions and the left anterior cingulate (non-significant cluster outcomes reported in Supplementary Table S2). Yeo's cortical parcellation atlas (2011) places the peak coordinates of this cluster (0, 20, 34) in the ventral attention network (VAN), more recently taxonomized as the mid-cingulo insular network (within the anatomical domain) or salience network (within the cognitive domain) (Uddin et al., 2019). Egger's test for publication bias was nonsignificant; bias = 2.17, *p* = .162, and funnel plots did not suggest the influence of small study effects (Figure 3).

Examining the original articles revealed increased functional connectivity to the median cingulate via the posterior cingulate cortex (PCC), a region canonically situated within the default mode network (DMN). Notably, studies within the sample exclusively reported increased connectivity between median cingulate effect regions and PCC seed regions. Therefore, the findings suggest that mindfulness training increased resting state functional connectivity between the default mode network and salience network.

Discussion

This meta-analysis is the first to systematically examine the effects of mindfulness-based training on resting state functional connectivity (rsFC), a neural marker of cognitive and emotion regulation. A systematic review of the literature revealed that rsFC has been sparsely investigated as a target of mindfulness training, with 12 studies meeting the eligibility criterion in the current review. Meta-analysis results partially supported our hypotheses, indicating that relative to training in one or another structurally equivalent (active control) program, mindfulness training increased functional connectivity to the midcingulate cortex (MCC), and that such connectivity was seeded to the posterior cingulate cortex (PCC). Results did not support our first hypothesis, which predicted enhanced cross-network connectivity between the FPCN and DMN as a mechanism of cognitive control. In support of our second hypothesis, these results suggest that mindfulness training strengthened cross-network connectivity between regions associated with the default mode network (DMN) and salience network (SN). Implications for null and supported findings are explored in the following sections.

Along with the frontoparietal control network (FPCN), the DMN and SN operate synergistically to support self-regulation, and aberrant coordination within and between these networks has been associated with emotional dysfunction, deficits in attentional control, and maladaptive stimulus-independent thinking (SIT) (e.g., rumination, worry, intrusive thought) (Menon, 2011; Feurer et al., 2021). It has been suggested that therapeutic outcomes of mindfulness are mediated by reorganization within and between such networks (Hölzel et al., 2011; Vago & Silbersweig, 2012; Tang et al., 2015; Vago & Zeidan, 2016); however, the precise neural targets of mindfulness are ill-defined, in no small part due to methodological differences between studies (e.g., in research designs, training protocols, and target populations) (Van Dam et al., 2018). Among explanations of mindfulness' neurocognitive mechanisms, the literature favors two competing theories, colloquially referred to as 'top-down' and 'bottom-up' models of mindful regulation. According to the top-down model, mindfulness recruits FPCN engagement to support the deliberate regulation of unwanted thoughts and emotions (Chiesa et al., 2013; Tang et al., 2015), and—through dynamic cross-network coupling—inhibits task-incongruent DMN activity (Cole et al., 2014). In contrast, bottom-up models suggest that mindfulness can operate automatically to modify thoughts and emotions without higher-level cognitive control (Ochsner et al., 2009). Specifically, such bottom-up regulation may diminish the propensity for rumination by reducing within-network DMN connectivity (Kucyi et al., 2014; Hamilton et al., 2015) or disrupting SN-DMN coordination associated with negative rumination (Andrews-Hanna et al., 2020). We suggest that the effect of mindfulness training on MCC-PCC connectivity may partially align with models of both top-down and bottom-up regulation.

Contrary to our prediction, this meta-analysis did not reveal involvement of FPCN cross-network connectivity, a finding that is inconsistent with prior neural characterizations of long-term meditators (Kemmer et al., 2015) and runs counter to theoretical explanations of the FPCN as a facilitator of mindful top-down regulation (Chiesa et al., 2013; Tang et al., 2015). However, our findings do not necessarily rule out mechanisms of top-down cognitive control. It has previously been suggested that executive control processes may operate via dissociable networks with distinct temporal profiles (Seeley et al., 2007; Dosenbach et al., 2008). According to this framework, the FPCN provides rapid, flexible feedback to lower-level systems, while the cingulo-opercular network [analogous to the salience network (Uddin et al., 2019)] functions to maintain cognitive control over longer epochs (Dosenbach et al., 2008). Included within the cingulo-opercular network is the MCC, the functional connectivity target region identified from our analysis. Otherwise referred to as the dorsal portion of the ACC (Allman et al., 2001), the MCC is distinguished by specialty Von Economo neurons (Watson et al., 2006; Correa-Júnior et al., 2020). Von Economo neurons—or spindle neurons—are characterized by long-distance signal transmission and heterogenous dendritic/spinal structures (Stevens et al., 2011; Allman et al., 2010), two features which appear to support cross-network information integration (Watson et al., 2006; Posner et al., 2007; Sheth et al., 2012; Correa-Júnior et al., 2020). It is plausible that mindfulness training may promote top-down cognitive control via cross-network integration with the MCC. Control via MCC projections may likewise mitigate cognitive strain on the FPCN, thereby

promoting a more sustainable, flexible mode of attention. Such an account may explain why we failed to detect functional connectivity between FPCN and DMN nodes.

Alternatively, increased PCC-MCC functional connectivity may support indirect (i.e., bottom-up) regulation through the promotion of meta-awareness. Embedded within the DMN, the PCC has classically been associated with the maintenance of internally-oriented mentation (Andrews-Hanna et al., 2014). However, the PCC may also play a critical role in attention regulation (Leech et al., 2011) and the general maintenance of vigilance (Hahn et al., 2007; Sämann et al., 2011). Evidence suggests that dorsal portions of the PCC may be involved in balancing internal and external attentional focus (Leech & Sharp, 2014) as facilitated through extensive cross-network connectivity (Margulies et al., 2009; Leech et al., 2012). In this vein, PCC connectivity with the MCC—a salience network hub—may serve to integrate information regarding the content, quality, and direction of attentional focus (i.e., meta-awareness). Thus, our finding of MCC-PCC connectivity may potentially underpin flexible cognitive faculties needed to observe internal states with open awareness.

Interpretation of the results reported here is limited by several factors. To date very few studies have examined rsFC outcomes of mindfulness, with even fewer implementing randomized controlled or quasi-experimental procedures. For this reason the meta-analysis pulls from a relatively small sample of 12 studies (MT $n = 226$; CT $n = 224$). Although such selectivity maintains the benefits of data quality and homogeneity of experimental conditions (i.e., mindfulness interventions), small samples also threaten generalizability as effects may be driven by only a few studies with shared experimental parameters (Müller et al., 2018). The extracted studies draw from heterogeneous populations—in terms of demographic characteristics, gender, and age—features which have shown to vary in both gray matter and connectome characteristics (Campbell et al., 2013; Ingallhalikar et al., 2014; Sha et al., 2019). Additionally, no study reported non-binary gender information and reports of racial/ethnic identity were omitted from 7 of the 12 studies included in our sample. The practice of demographic underreporting is a substantial challenge in the field of mindfulness research (and psychological research more broadly), with important implications for health inequities (Eichel et al., 2021). Future researchers should prioritize responsible reporting and recruitment practices to address such disparities (Eichel et al., 2021; Sabik et al., 2021).

The duration and therapeutic focus of mindfulness interventions likewise warrant consideration. Although the mindfulness interventions were standardized and well-matched against active control programs, these studies report a wide range of intervention durations (3 days - 16 weeks) with different degrees of intensity (i.e., retreat versus remote-delivered trainings) and therapeutic focus (e.g., PTSD, parent-focused stress reduction). There is currently little research examining the dose-response relation for mindfulness-based treatments; however, a recent meta-analysis of this topic suggests that brief trainings may be equally as effective as longer interventions for the treatment of stress, depression, and anxiety (Strohmaier, 2020). Nevertheless, the relation between mindfulness training dose and neuroplasticity remains poorly understood, a matter that is further complicated when applied to clinical and aging populations with atypical connectomes (Geerligs et al., 2015; Sha et al., 2019).

Interpretation is likewise limited by a priori seed selection, which was requisite for all included studies (see protocol from Kaiser et al., 2015). This study failed to detect significant FPCN cross-network connectivity, and while this null effect may stem from erroneous theoretical assumptions, it may instead be the consequence of preferencing seeds within the DMN. Behavioral neuroimaging studies have previously shown strong functional coupling between the FPCN and DMN across multiple tasks (e.g., Farb et al., 2007; Spreng et al., 2010; Fleming & Dolan, 2012), and one study recently demonstrated how robust co-activation of FPCN and DMN regions may obscure detection of group effects (Dixon et al., 2021). Further research is needed to definitely determine if and how mindfulness training interacts with FPCN neurocircuitry during task-related and resting brain states.

Finally, it warrants noting that there is currently no standard classification system for large-scale functional networks. The lack of universal nomenclature presents a significant barrier to interpreting neural outcomes, especially given the multitude of naming schemes (Uddin et al., 2019) and inconsistent application of common labels (see meta-analysis of executive control network topography; Witt et al., 2021). We use the functional network terms “frontoparietal control network”, “default mode network”, and “salience network” primarily due to their ubiquity in cognitive neuroscience (Uddin et al., 2019) and the mindfulness literature. Nevertheless, such naming conventions based on functional properties are problematic for the reasons described above. We recommend that future research move towards more transparent network taxonomies incorporating anatomical properties (see Uddin et al., 2019).

This meta-analysis highlights the potential value of rsFC as a window into understanding the mechanisms of mindfulness. However, research on this topic is in its early stages, and considerably more research is necessary to qualify specific rsFC effects as mechanistic targets of mindfulness training. Without additional research, the effects of mindfulness on resting state cognition remains speculative. Researchers may consider novel sampling methods including lab-based phenomenological reporting (e.g., Hasenkamp et al., 2012) and ecological momentary assessment, a method used to capture day-to-day lived experiences (Berkman & Falk, 2013; Gillan & Rutledge, 2021). Investigators should additionally consider examining multiple representations of connectivity—including effective connectivity,

white matter connectivity, and dynamic connectivity—which probe different features of brain network organization (e.g., directional effects; temporal dynamics, etc.). The comparison of such representations has the potential to reduce ambiguity and improve interpretation of connectivity-based effects (Bijsterbosch et al., 2020).

Further research is also needed to determine the relevance of rsFC plasticity for different psychiatric conditions. The successful use of network neuroscience for clinical diagnosis and treatment is a lofty goal, which will require overcoming considerable methodological challenges (see Woo et al., 2017; Douw et al., 2019). Such research necessitates reliability and reproducibility; however, preprocessing and analysis procedures may vary significantly among studies based on individual research questions. Nevertheless, researchers can promote standardization of analysis techniques through commitment to open science practices in which scripted pipelines and nonthreshold brain images are publicly catalogued (for recommendations, see Bijsterbosch et al., 2020).

Conclusion

Resting state neural indices have potential to elucidate the rich subtleties of internal experiences, with important implications for those suffering from rigid or negative inner dialogues. According to Buddhist perspectives, mindfulness offers a window into exploring the qualities of conscious experience and—through heightened awareness of such mental states—enables their adaptive transformation (Vago & Silbersweig, 2012;). However, it remains ambiguous how mindfulness practice can be optimized to reduce suffering in heterogeneous populations, both healthy and clinical (Creswell, 2017; Britton et al., 2018; Eichel et al., 2021). The current meta-analysis aimed to elucidate the nature of mindfulness training effects by focusing on neural indices of the resting mind. Results indicated strengthened MCC-PCC connectivity as a product of mindfulness. Although interpretation of this effect requires more experimental research, results may nevertheless advance the science of mindfulness and its impact on the resting brain.

Methods

Literature Search

A comprehensive literature search was conducted using the keywords *rest*(-ing)*, *connect*(-ivity)*, *default mode*, *mindfulness*, *meditation*, *MBSR* [Mindfulness-based stress reduction], and *MBCT* [Mindfulness-based cognitive therapy] to search for matching literature from the following databases: MEDLINE/PubMed, ERIC, PSYCINFO, ProQuest, Scopus, and Web of Sciences. Texts were screened by four reviewers and considered for inclusion if they reported resting state functional connectivity outcomes derived from functional magnetic resonance imaging (fMRI) modalities. Further, all included studies were randomized controlled trials or used quasi-experimental (e.g., matched control) designs in which standardized mindfulness-based interventions (MBSR (Kabat-Zinn, 2003), MBCT (Segal et al., 2018)) were compared to an active control condition.

Studies were excluded if they met one or more of the following criteria: (1) experimental interventions predominantly featured training elements other than mindfulness meditation (e.g., yoga, transcendental meditation, loving-kindness or compassion meditation, tai chi; integrative body-mind training); (2) the study design lacked an active control condition or used a cross-sectional design; (3) resting state functional connectivity (rsFC) group contrasts were not reported; (4) seed-based rsFC methods were not used or seed-based rsFC indices were not reported.

The systematic literature review identified 7,092 records, from which 7,071 were excluded upon abstract review (see PRISMA flow diagram in Figure 1). Full-text examination of the remaining 21 studies for eligibility yielded a sample of 12 eligible publications (Brewer et al., 2011; Wells et al., 2013; Taren, 2015; Taren et al., 2015; Creswell et al., 2016; King et al., 2016; Shao et al., 2016; Kral et al., 2019; Kwak et al., 2019; Turpyn et al., 2019; Van der Gucht et al., 2020; Chumachenko et al., 2021; Rahrig et al., 2021). The final sample of studies reported data from 226 participants assigned to mindfulness training and 204 participants assigned to an active control program.

Data Extraction and Coding

The meta-analysis was coordinate-based (for example see Kaiser et al., 2015), in which extracted coordinates reflected locations of significant group differences in resting state functional connectivity across time. Given that all studies used seed-based rsFC analyses, coordinates were categorized as belonging to either seed anatomy or effect anatomy. Using this coding scheme, 11 sets of seed coordinates were extracted, with coordinates reflecting each seed anatomy's reported center of mass. In the instance that seed anatomy coordinates were not reported because the seed region was defined from a standardized atlas or subject-specific spatial map, the center of mass was estimated using meta-analytic maxima reported from the open source platform, neurosynth.org (Yarkoni et al., 2011). All studies reported peak coordinates of significant between-group effects, yielding a total of 65 effect coordinates. After extracting seed and

effect coordinates, all coordinates were categorized into rsFC networks as defined from a standardized network cortical parcellation atlas (Yeo et al., 2011). Effects were likewise characterized by direction of effect with the term hyperactivation reflecting relatively greater rsFC effects in the mindfulness group (MT > CT), and hypoactivation indicating relatively greater rsFC in the control group (CT > MT). In addition to main effects, demographic data and intervention characteristics were extracted for review. Effects were extracted by four independent reviewers who collected data from independent reports.

Interrater Reliability

We conducted a two-way random-effects ICC modeled with absolute agreement. Specifically, we tested for significant effects of rater ID on each quantitative measure. ICC estimates were within acceptable range ($ICC > .6$; $p < .005$), indicating a high degree of rater agreement. Next, unweighted Cohen's kappa was calculated to examine reliability of extracted categorical variables. Results indicated substantial agreement (Altman, 1999; Landis & Koch, 1977) between the raters' judgements, $k = .741$ (95% CI .182 to .884). Finally, z statistics were converted to two-sample t-test statistics, assuming equal variances in both conditions. If records did not report z statistics or two-sample t-test statistics, p values were used to estimate t-test statistics used in the meta-analysis.

Voxel-based meta-analysis

Voxel-based meta-analysis was conducted using seed-based *d* mapping (SDM-PSI version 6.21) with permutation of subject images (Albajes-Eizagire et al., 2019b). Unlike traditional meta-analytic approaches which test for the presence or absence of peaks of statistical significance (i.e., null hypothesis testing), seed-based *d* mapping (SDM) uses multiple imputation to model effect sizes for each study before conducting a random-effects meta-analysis. Notably, SDM has the advantage of controlling false positive and false negative rates through subject-based permutation tests (Winkler et al., 2014) and threshold-free cluster enhancement (Smith & Nichols, 2009).

SDM preprocessing was first used to convert *t*-values of peak coordinates into Hedge's *g* effect sizes. Study-level images of upper and lower bounds of probable effects were then constructed for all voxels using multiple imputation (Rubin, 2004; Albajes-Eizagire et al., 2019a) with anisotropic Gaussian kernels. Using SDM we then calculated most likely effect size and standard error via multiple imputations of Maximum Likelihood Estimation (MLE) with a jackknife procedure. Finally, FWE corrections were performed via subject-based permutation testing and TFCE-corrected effect sizes were calculated to estimate group differences. Main analytic findings were scrutinized for small study effects and excess significance (i.e., publication bias) through Egger's tests and examination of funnel plots.

Declarations

Author Contributions

The authors confirm contribution to the paper as follows: study conception and design: HR, KWB; data extraction and curation: MP, AA, NL; analysis and interpretation of results: HR; KWB, DRV; draft manuscript preparation: HR, KWB, DRV; study conception and design: HR, KWB

Acknowledgements and Funding Information

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability statement

The datasets generated during and/or analysed during the current study are available in the neurovault repository, <https://identifiers.org/neurovault.image:768613>

Review protocol is not registered and can only be accessed upon request.

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Tables

TABLE 1. *Demographic Characteristics of Mindfulness and Control Conditions*

Reference	Population Description	Program Description		<i>n</i> analyzed		Age <i>M</i> (<i>SD</i>)		Biological sex <i>n</i> (%)	
		MT	Control	MT	Control	MT	Control	MT	Control
Brewer et al., 2011	Individuals with > 10 y mindfulness meditation experience vs. meditation-naïve controls	NA - quasi-experimental design		<i>n</i> =13	<i>n</i> =12	51.5 (6.8)	49.4 (6.2)	Male 5 (41.7%)	Male 6 (50%)
								Female 7 (58.3%)	Female 6 (50%)
Chumachenko et al. (2021)	Individuals who recently lost weight intentionally and were engaged in weight loss maintenance	Mindfulness Based Stress Reduction (MBSR)	Structurally equivalent Healthy Living Course	<i>n</i> =28	<i>n</i> =23	44.5 (9.70)	44.5 (10.65)	Male 7 (24%)	Male 4 (13%)
								Female 22 (76%)	Female 24 (87%)
Creswell et al. (2016)	Stressed unemployed community adults	3-day mindfulness meditation retreat	Structurally equivalent relaxation training intervention	<i>n</i> =17	<i>n</i> =17	37.94 (10.96)	41.00 (9.55)	Male 11 (61.11%)	Male 9 (52.94%)
								Female 7 (38.89%)	Female 8 (47.06%)
King et al. (2016)	Male combat veterans with diagnosed PTSD	16-week nontrauma-focused mindfulness-based exposure therapy; incorporates elements from MBCT and PTSD psychoeducation	16-week present-centered group therapy; controls for nonspecific therapeutic factors	<i>n</i> =12	<i>n</i> =8	32.43 (7.54)	31.67 (10.14)	Male 14(100%)	Male 9(100%)
								Female 0 (0%)	Female 0 (0%)
Kral et al. (2019)	Healthy meditation-naïve adults	MBSR	Structurally equivalent Health Enhancement Program (HEP)	<i>n</i> =31	<i>n</i> =34	41.4 (12.9)	43.6 (13.1)	Male 13 (41.94%)	Male 12 (35.29%)
								Female	Female

								18 (58.06%)	22 (64.71%)
Kwak et al. (2019)	Healthy office workers and graduate students	3-day mindfulness meditation retreat at a Buddhist temple	3-day relaxation retreat without structured activities	<i>n</i> =30	<i>n</i> =17	30.63 (4.97)	31.71 (5.02)	<i>Male</i> 6 (20%)	<i>Male</i> 5 (29.41%)
								<i>Female</i> 24 (80%)	<i>Female</i> 12 (70.59%)
Shao et al. (2016)	Healthy elderly adults with no prior meditation or relaxation training experience	8-week attention- based compassion meditation training	Structurally equivalent relaxation training	<i>n</i> =21	<i>n</i> =19	64.78 (2.71)	64.68 (2.19)	<i>Male</i> 7 (30%)	<i>Male</i> 8 (36%)
								<i>Female</i> 16 (70%)	<i>Female</i> 14 (64%)
Taren et al. (2015a)	Stressed unemployed job-seeking community adults	3-day mindfulness meditation retreat	Structurally equivalent relaxation training intervention	<i>n</i> =17	<i>n</i> =17	37.94 (10.96)	41.00 (9.55)	<i>Male</i> 11 (61.11%)	<i>Male</i> 9 (52.94%)
								<i>Female</i> 7 (38.89%)	<i>Female</i> 8 (47.06%)
Turpyn et al. (2019)	Stressed mothers of adolescent children	8-week parenting focused mindfulness intervention based on MBSR	Structurally equivalent parenting education intervention	<i>n</i> =10	<i>n</i> =10	<i>Combined Programs</i> 48.5 (7.62)		<i>Male</i> 0 (0%)	<i>Male</i> 0 (0%)
								<i>Female</i> 10 (100%)	<i>Female</i> 10 (100%)
Van der Gugt et al. (2020)	Breast cancer survivors reporting cognitive impairment	8-week mindfulness- based intervention developed for patients with cancer	Waitlist controlled condition	<i>n</i> =12	<i>n</i> =13	43.89 (6.03)	47.4 (5.45)	<i>Male</i> 0 (0%)	<i>Male</i> 0 (0%)
								<i>Female</i> 18 (100%)	<i>Female</i> 15 (100%)

Wells et al. (2013)	Adults with mild cognitive impairment	MBSR	Care as usual	<i>n</i> =8	<i>n</i> =5	73 (8.00)	75 (7.00)	<i>Male</i> 3 (33%)	<i>Male</i> 6 (60%)
								<i>Female</i> 6 (67%)	<i>Female</i> 2 (40%)
Rahrig et al. (2021)	Stressed, meditation- naive community adult	2-week remote delivered mindfulness training	Structurally equivalent training in active coping techniques	<i>n</i> =11	<i>n</i> =12	33.36 (7.30)	35.67 (8.54)	<i>Male</i> 2 (18%)	<i>Male</i> 6 (50%)
								<i>Female</i> 9 (82%)	<i>Female</i> 6 (50%)

Table 2.

<i>MNI coordinate</i>	<i>SDM-Z</i>	<i>P</i>	Description
0,20,34	1.898	0.028856218	Left median cingulate / paracingulate gyri, BA 24
Brain region			Voxels
Left median cingulate / paracingulate gyri, BA 24			13
Right median cingulate / paracingulate gyri, BA 24			12
Left median cingulate / paracingulate gyri			2
Left anterior cingulate / paracingulate gyri, BA 24			2
Right median cingulate / paracingulate gyri			1

Figures

Figure 1

The top figure portrays the location of the PCC ROI seed. The bottom figures show a 3D map of voxelwise z-scores, with significant cluster effects localized to the bilateral paracingulate gyri.

Figure 2

Funnel plot indicating relative symmetry in the scatter of studies based on effect index, i.e., residual (x-axis) and sample size index, i.e., precision (y-axis). Plot symmetry suggests the absence of publication bias due to trial size.

Figure 3

PRISMA flow diagram depicting records identified and screened for eligibility for the meta-analysis.

Supplementary Files

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