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Signal or noise: brain network interactions underlying the experience and training of mindfulness

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A broad set of brain regions has been associated with the experience and training of mindfulness. Many of these regions lie within key intrinsic brain networks, including the executive control, salience, and default networks. In this paper, we review the existing literature on the cognitive neuroscience of mindfulness through the lens of network science. We describe the characteristics of the intrinsic brain networks implicated in mindfulness and summarize the relevant findings pertaining to changes in functional connectivity (FC) within and between these networks. Convergence across these findings suggests that mindfulness may be associated with increased FC between two regions within the default network: the posterior cingulate cortex and the ventromedial prefrontal cortex. Additionally, extensive meditation experience may be associated with increased FC between the insula and the dorsolateral prefrontal cortex. However, little consensus has emerged within the existing literature owing to the diversity of operational definitions of mindfulness, neuroimaging methods, and network characterizations. We describe several challenges to develop a coherent cognitive neuroscience of mindfulness and to provide detailed recommendations for future research.

Keywords: mindfulness; meditation; functional connectivity; brain networks

Societal interest in mindfulness is growing rapidly, largely due to evidence of a strikingly diverse set of benefits that stem from its practice, including improved vigilance, working memory, emotional regulation, executive function, and metacognition; reduced mind wandering; and recovery from psychological disorders such as depression, anxiety, or posttraumatic stress disorder.[1–9] In parallel with the now worldwide scientific effort to document these and other benefits, considerable research has also explored the neural basis underlying the experience and training of mindfulness. Within the last 5 years, particular focus has been directed toward understanding the effect of mindfulness on patterns of functional connectivity (FC) between distributed brain regions. This effort has leveraged ongoing advances in neuroimaging methods and cognitive neuroscience, including a rapidly unfolding understanding of how distributed brain regions collaborate as networks that, in turn, interact with other networks.

Particular attention has been given to the default, executive, and salience networks, which have been identified as functional networks that likely underlie the experience and training of mindfulness.[10] Yet numerous methodological challenges have forestalled consensus about how mindfulness is related to patterns of FC within and between these networks. The considerable diversity in both methods and findings makes it nearly impossible to separate signal from noise. Here, we systematically review and evaluate current scientific understanding by (1) identifying the fundamental challenges in defining, measuring, and training mindfulness; (2) reviewing what is known about the anatomical and functional bases of the default, executive, and salience networks; (3) summarizing the key methodological challenges in using neuroimaging to determine network interactions underlying mindfulness; (4) providing a systematic and exhaustive review of the existing literature; and (5) offering detailed methodological considerations that can guide future research.

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The diversity of mindfulness

Perhaps the greatest challenge to developing a coherent cognitive neuroscience of mindfulness is the diversity of ways in which mindfulness is defined and investigated. Debate within the psychological and brain sciences over the most privileged definition of mindfulness has continued for more than 2 decades.[11–15] The most widely circulated definition is "paying attention on purpose, in the present moment, and nonjudgmentally, to the unfolding of experience moment to moment."[11] The widespread adoption of this definition indicates that many researchers view mindfulness as a multidimensional construct including elements of intention, attention, evaluation, and present-mindedness. Yet disagreement persists regarding the specific elements that are relevant, and numerous validated questionnaires exist to measure these divergent perspectives on dispositional levels of mindfulness. These scales include as few as one and as many as five subscales, drawing from a diverse set of elements, including focused attention, nonjudging, acceptance, curiosity, nonreactivity, decentering, and either describing or labeling experiences as they occur.[16–20] Still greater complexity arises from the diversity of practices that have been used to cultivate mindfulness, including practices that fall into categories conventionally described as *focused attention* and *open monitoring*.[21] Meditations that emphasize focused attention typically involve the deliberate restriction of attention to a chosen object—such as the sensations of breathing, the taste of food, or the tactile sensations in one's feet while walking—and the voluntary redirection of attention each time it lapses. By contrast, open-monitoring practices emphasize observing experience from moment to moment without any deliberate focus of attention and are sometimes described as *choiceless awareness*. Given this diversity, here we use the term "mindfulness" to refer generally to a category of experiences and practices that have been described as mindfulness within the existing literature.

This diversity is a major challenge for research into the neural basis of mindfulness. Different mindfulness scales are associated with unique patterns of FC,[22] and different meditation practices can lead to distinct and even opposing patterns of brain activation.[23,24] Furthermore, a variety of different methodological designs have been used to investigate the patterns of FC associated with mindfulness, including correlational studies, longitudinal training studies, and cross-sectional studies comparing expert meditators to either nonmeditating controls, beginning meditators, or somewhat less experienced experts.[22,25–27] Given this diversity, one might reasonably doubt that a coherent cognitive neuroscience of mindfulness would emerge. Alternatively, one might argue that a great deal is shared in common between different measures and practices, and that diverging methods could provide complementary and converging accounts of the mindful brain. To examine this possibility, we reviewed the existing literature that relates mindfulness in its various manifestations to the FC between default, executive, and salience networks.

Mindfulness and intrinsic brain networks

Mindfulness practices in their various forms require the control of attentional focus, the inhibition of elaborative thought, and the reorientation or disengagement of attention after lapses. These capacities are partially rooted in the operation of three intrinsic brain networks: the default network, the executive network, and the salience network. Much of the neuroimaging research that has assessed the impact of mindfulness on brain function has implicated these networks, either explicitly through planned analyses constrained to regions within these networks or through whole-brain analyses. We now introduce the anatomical and functional characterizations of these networks to provide context for their involvement in mindfulness research.

The default network

The default network may be particularly relevant to the experience and training of mindfulness given its role in many aspects of spontaneous and deliberate thought. Mindfulness practice in its various forms emphasizes altering the frequency, appraisal, and/or content of thoughts, and thus may affect default network function. The default network comprises several regions that were originally noted for their tendency to deactivate together during goal-directed tasks,[28] yet further research has demonstrated that these regions show coherent activity not simply in their task-induced deactivations but also during the performance of a variety of tasks requiring internally generated thought. Regions of the default network deactivate during some tasks but are recruited

Table 1. Key cortical regions within the default, executive, and salience networks

Network	Key cortical regions	Abbreviation	Brodmann area(s)
Default			
	Medial prefrontal cortex	mPFC	9, 10, 11
	Posterior cingulate cortex	PCC	23, 31
	Retrosplenial cortex	Rsp	26, 29, 30
	Parahippocampal cortex	PHC	36
	Superior frontal gyrus	SFG	4, 6, 8
	Inferior frontal gyrus	IFG	44, 45, 47
	Angular gyrus	AG	39
	Temporoparietal junction	TPJ	39, 40, 22
	Temporal pole	TP	38
Executive			
	Dorsolateral prefrontal cortex	dlPFC	9, 46
	Posterior parietal cortex	PPC	5, 7
Salience			
	Dorsal anterior cingulate cortex	dACC	24, 32, 33
	Anterior insula	aINS	N/A
	Supramarginal gyrus	SMG	40
	Superior temporal gyrus	STG	22, 41, 42

NOTE: Brodmann areas are derived from cytological distinctions and therefore serve as useful anatomical landmarks, yet they do not perfectly correspond to functional distinctions.

during others, making a definition of the network based on task-related deactivation patterns untenable. However, during the unconstrained setting of the resting state, several intrinsic functional brain networks can be observed by assessing temporal correlations among the activities of regions throughout the brain.[29,30] One of these intrinsic networks shares substantial overlap with regions previously observed to be deactivated during external tasks, and as such this default network appears to be functionally integrated and consistent across individuals. The default network includes regions of the medial prefrontal cortex (mPFC; including the dorsomedial PFC, the rostral anterior cingulate cortex, and the anterior and ventral mPFC), the medial parietal cortex (posterior cingulate and retrosplenial cortices), and the medial temporal lobe (hippocampus and parahippocampal cortices), as well as lateral regions of the frontal cortex (superior frontal cortex and inferior frontal gyrus), the parietal cortex (angular gyrus and temporoparietal junction), and the temporal cortex (extending to the temporal poles) (Table 1). These regions show additional association with portions of the cerebellum (Crus I and II subdivisions) and the striatum (posterior putamen and medial caudate).[30,31]

The default network is activated during tasks involving different kinds of internally focused cognition: retrieval of episodic, autobiographical, or semantic information; thinking about or planning for the future; imagining novel scenes or situations; inferring mental states in others; and self-reference or self-appraisal.[32,33] The default network is also transiently engaged during externally focused tasks.[34–36] In this case, such activation likely reflects the process of mind wandering, in which one's attentional focus shifts away from task-relevant stimuli toward unrelated, self-generated thoughts.[37] Experience sampling studies suggest that 30–50% of our waking day is spent engaged in mind wandering.[38–40] Such thoughts are remarkably heterogeneous in nature with regard to their personal significance, temporal orientation, valence, and representational format (e.g., visual imagery versus inner monologue).[41]

The heterogeneous nature of self-generated thought suggests complexity and/or modularity in the organization of the default network. Recent clustering approaches suggest that the default network comprises at least three interacting components (although potentially many more components may be observable depending on the partitioning principle[32]): a left-lateralized *dorsal medial subsystem* composed of the dorsomedial PFC, the temporoparietal junction, the lateral temporal cortex, the inferior frontal gyrus, and the lateral superior and ventral frontal cortices; a *medial temporal subsystem* composed of hippocampal and parahippocampal regions, the retrosplenial cortex, and the ventromedial PFC; and a *midline core system* composed of the anterior medial PFC (amPFC), the posterior cingulate cortex (PCC), and possibly additional regions of the superior frontal gyrus, the bilateral angular gyrus, and the anterior temporal lobes.[30,36]

In their recent review article, Andrews-Hanna *et al.*[31] performed a meta-analysis to determine the cognitive processes supported by each of these three default subdivisions. They found that the dorsal medial subsystem is most associated with mentalizing, social cognition, and comprehension and semantic/conceptual processing.[32,33,42–45] Regions within this subsystem may also serve a more general role in the retrieval of relevant conceptual and social knowledge. The medial temporal subsystem is more strongly associated with past- and future-oriented autobiographical thought, episodic memory, and contextual retrieval. It is also thought to be crucial for the active construction of mental simulations.[32,42,46] The core network, which shares reciprocal connections with the other subsystems, is associated with self-related processes and emotion/evaluation processes. The core system is an important zone of integration, as it shares anatomic and functional connections with many other brain systems. Within the core system, the PCC has been linked to autonomic arousal and awareness and to monitoring for behaviorally relevant information.[47–49] The PCC also demonstrates the most substantial FC with medial temporal regions of the default network.[50] The anterior lateral temporal cortex plays a major role in conceptual processing and shares connectivity with the angular gyrus, which exhibits multimodal connectivity with a wide range of regions involved in perception, attention, and action.[51] Finally, the amPFC is strongly connected to the PCC and other default subsystems,[36] as well as limbic and subcortical regions associated with affective and autonomic regulation.[52] It is highly involved in self-relevant processing, particularly of information with affective components. As such, the amPFC, and the core system as a whole, is well suited to integrate relevant internal or external information with one's prior semantic and/or episodic knowledge and current affective state, thus constructing a representation of the personal meaning of a stimulus or situation.

The default network is therefore a heterogeneous system of interacting subnetworks capable of supporting a diversity of cognitive processes. Given its role in internally focused cognition, aspects of the default network will likely be influenced by mindfulness practices that alter the frequency, content, or appraisal of thoughts. However, it is likely that mindfulness training may have nonuniform effects on the various subnetworks and regions that compose this highly distributed network. It is also likely that mindfulness practices that emphasize focused attention will affect the default network differently than those that emphasize open monitoring of any thoughts or sensations that arise.

The executive network

The executive network may be relevant to mindfulness given its general role in goal-directed behavior. The executive network (otherwise known as the "central executive" or "executive control" network) represents a set of brain regions that, often in contrast to default network regions, become more active during cognitively demanding tasks.[34,53–59] Executive network functioning is thought to be crucial for several key elements of cognition: the maintenance and manipulation of information in working memory, judgment and decision making, responding to changing task demands, inhibition, planning, and the control of the focus of attention. Many of these elements are also important aspects of the cognitive operations required to train and sustain mindfulness. For example, the regulation of attention is involved in all forms of mindfulness practice, although this control may be implemented in somewhat different ways according to the type of mindfulness practice. Focused attention practices emphasize sustained attention to a particular object and may therefore require the inhibition of elaborative conceptual thought and the inhibition of exogenous redirection of attention to salient perceptual events. Open-monitoring practices emphasize the avoidance of sustained attentional engagement with any particular mental or perceptual object, and therefore share the need to inhibit elaborative conceptual thought. However, open monitoring does not require the inhibition of exogenous redirection of attention, but instead involves the inhibition of the tendency to sustain attention on arising perceptual or mental events.

The executive network comprises main nodes in the dorsolateral PFC (dlPFC) and posterior parietal cortices (Table 1).[34,53–55,57,58,60] As such, it overlaps with the more broadly defined frontoparietal control network (FPCN).[30,58,60–63] However, while the FPCN is often treated as a single entity,[60,62] recent work has demonstrated heterogeneity of function within the FPCN, suggesting that it may be more appropriate to consider the more anatomically constrained executive network as a distinct functional network.[53,58,63]

Early descriptions of the executive network placed considerable emphasis on its task-related activation, as well as the observation that its activity is often negatively correlated with activation in the default network.[29,53,56] However, it is now clear that the default network is not simply activated in the absence of a task, but rather is involved in the performance of tasks involving internally generated stimuli or information. The executive network enables maintaining, manipulating, and selectively attending to task-relevant information, and recent research indicates that this is also true during internally focused tasks.[62,64,65] For example, goal-directed cognition that is internally focused—like autobiographical planning—involves the coactivation of the executive and default networks.[62] Some regions within both networks also show greater activation during mind-wandering episodes than during task focus, especially when mind wandering occurs without meta-awareness.[34] This suggests that the executive network can be flexibly recruited to support either externally focused tasks or internally focused thought.

The salience network

The salience network may be relevant to the experience and training of mindfulness, given its role in both interoception and redirecting attentional resources. Its main cortical nodes are the dorsal anterior cingulate cortex (dACC) and the bilateral anterior insulae (aINS; Table 1),[30,53–55,66,67] although additional regions such as the supramarginal and superior temporal gyri are also associated with the salience network but not studied in relation to it as frequently.[30,53,68] These cortical salience hubs also have extensive connectivity with many subcortical sites, including the amygdalae, dorsomedial thalamus, hypothalamus, periacqueductal gray, and substiantia nigra/ventral tegmental areas.[53] Multiple investigations have pointed toward a role of the salience network in the detection of behaviorally relevant external stimuli.[55,67–69] Additionally, regions of the salience network activate in response to subjectively salient information, whether the dimension is cognitive, homeostatic, or emotional.[53,54,70,71] The salience network is built upon limbic and paralimbic structures that are known to underlie interoceptive and autonomic processing[70,71] and that also receive multimodal sensory information. This organization makes the salience network well suited to be able to integrate sensory and cognitive information with visceral, autonomic, and hedonic "markers" of salience.[72]

Evidence suggests that the salience network is also involved in the dynamic switching between activation of the executive and default networks. The right aINS appears to play a causal role in activating the executive network and deactivating regions of the default network, acting as a causal outflow hub in its functional relationship with these two networks.[55] Its activation peaks also tend to precede activation peaks in executive and default network regions.[55] While perspectives differ on the precise method by which subregions of the salience network modulate cognitive control,[54] it is generally agreed that the salience network plays an active role in modulating the allocation and direction of attentional resources in accordance with the salience of internal and external stimuli; a primary aspect of this process involves its capacity to inhibit default network activity and direct executive network processing toward appropriate task-related targets. In patients with traumatic brain injury, structural damage within the salience network led to failures to deactivate the default network and failures of inhibitory cognitive control.[73] Similarly, hallucinatory symptoms in schizophrenia have also been associated with aberrant functional relationships between salience and default and executive regions, specifically in the reduction of the insula's influence in modulating activity in these other networks.[74]

Based on these findings, the salience network likely plays a critical role in the maintenance of states of mindfulness. The salience network is involved in the evaluation of the subjective salience of both external and internal aspects of experience. By modulating the allocation of attentional resources, the salience network can influence the controlled processing of the executive network and perhaps also the occurrence of spontaneous thoughts supported by the default network. In the case of open-monitoring practices, salience network function may determine the extent to which particular aspects of experience become consciously attended, and importantly, the extent to which executive resources become deployed toward that aspect of experience. In focused attention practices, the salience network's modulatory capacity is likely particularly important, as it may trigger the inhibition of default network activity and direct the allocation of attention toward the aspect of experience that is intended to be the singular object of attention.

Default, executive, and salience networks in relation to mindfulness research

Lines of research examining the neural correlates of mindfulness have rightfully focused largely on the functional relationships between the default, executive, and salience networks. The default network is highly involved in self-generated and internally oriented thought and is known to become active during lapses of attention away from a primary task. In the case of mindfulness and/or meditation, default network activity may thus provide an important marker of either mind wandering during a period of intended focus or of self-referential focus and internally directed attention. Executive network activity reflects the maintenance of task goals and directives, as well as the goal-directed focus of attention. However, executive and default network activations in concert may reflect something else entirely: the recruitment of executive resources in support of internal cognition or mind wandering. The function of the salience network may be especially crucial during mindfulness practice or in the cultivation of mindfulness, as it is involved in deciphering the appropriate selection of salient information in the environment and redirecting attentional resources to task-relevant targets through modulating activity in the default and executive networks.

Methodological challenges in using neuroimaging to determine network interactions underlying mindfulness

Issues in task selection and relative task demands

The effect of mindfulness on network dynamics almost certainly depends on the specific task in question. For instance, mindfulness tasks emphasizing focused attention on a sensory object may involve the inhibition of default network activity in order to maintain a singular focus, whereas open-monitoring practices that emphasize awareness of any arising sensations or thoughts may elicit a different pattern of default network activity.[10] Thus, the particular form of mindfulness practice being implemented in the scanner likely influences the specific pattern of brain network dynamics.[23] There is wide variation in the mindfulness practices that participants complete in the scanner within the existing literature, which reduces the likelihood that studies with similar research objectives will produce converging results. In addition to mindfulness tasks, resting-state scans are also commonly employed, but subtle differences exist in the instructions given to participants for these scans as well. Carryover effects between tasks may also exist when participants alternate between different mindfulness practices and/or rest. Finally, an additional challenge is that growing mindfulness expertise may be associated with nonlinear changes in network dynamics that could interact in complex ways with task demands. For instance, relatively high salience network activity may initially be necessary to monitor for frequent distraction but may become less necessary as attentional stabilization is achieved. In principle, this scenario might lead studies with relatively short mindfulness training to find increases in FC between salience and default regions, whereas extensive training could lead to decrease in FC between these same regions.

Network definition

As explored above, the networks of interest in mindfulness neuroimaging research are not necessarily clearly delineated. The executive and salience networks, for instance, are often discussed as elements of a more broadly defined FPCN rather than treated as separate functional entities. The default network, conversely, may itself be separable into additional subsystems. Scientific understanding of the manner in which these subsystems interact and the conditions in which such interaction occurs is still quite limited.

The precise boundaries between subsystems and entire networks have also not been definitively established. For instance, differences in the anatomical extent of the default network have been reported;[30,36] while these are likely due to differences in anatomical partitioning and clustering methodologies, such variance makes the constrained assessments of a particular network subject to the selection of a somewhat arbitrary criterion for network definition. Furthermore, endeavors to divide networks further and to examine interactions between components of a single network or elements of multiple networks have led to the conceptualization of particular nodes as "dual aligned." In this case, a region is associated with multiple subsystems of a network (e.g., the PCC in the default network[36]) or exhibits significant FC with nodes from multiple networks (such as the dACC, a region of the salience network, which shares connectivity with the default, executive, and dorsal attention networks[63]). This creates additional issues when defining networks or subnetworks, as some nodes carry joint membership. This issue has not arisen strictly from methodological discrepancies, as dual-aligned nodes represent real and necessary points of interaction between otherwise independent brain networks; it does, however, pose a practical hurdle in network selection and in comparing results from studies that have employed different selection choices.

Network science within the brain is still a relatively new endeavor. It has been less than 15 years since the discovery of the default network,[28] and network/graph theory approaches for analyzing neuroimaging data are arguably even newer. As such, our understanding of the role of networks within the brain is still developing. Ten years ago, we were able to use FC approaches to distinguish between task-positive and task-negative intrinsic networks,[29] yet today we can distinguish between at least seven basic intrinsic brain networks, although arguably even more can be characterized. The distinction between the executive and salience networks was first made less than 10 years ago.[53] Contemporary efforts to describe the organization of brain networks have led to even greater fractionation (as can be seen within the default network[75]), and this push will likely continue in the near future as imaging resolutions and methodological approaches continue to advance.

Mindfulness and functional connectivity

Table 1 presents a summary of the key brain regions associated with the default, executive, and salience networks. Tables 2 and 3 present detailed accounts of significant findings regarding FC within (Table 2) and between (Table 3) the default, executive, and salience networks from existing mindfulness neuroimaging research. It is clear upon inspection that direct replications of findings are rarely observable across studies. Amid the noise, however, two results appear across several studies.

First, mindfulness may be associated with an increase in resting-state FC between default network seed regions containing the PCC and default regions within the ventromedial prefrontal cortex.[a] Among studies that have specifically seeded the PCC (or the PCC in combination with other midline default regions) for a resting-state scan, three of the four studies report a significant increase in FC with the ventromedial prefrontal cortex (vmPFC). The fourth study did not replicate this result, although partial correlation analyses between the PCC and the vmPFC also displayed a trend toward increased FC.[26,b] This convergence appears despite considerable diversity in how mindfulness was operationalized, including a mindfulness training intervention[76] and the comparison of highly experienced meditators to either novices[77] or less-experienced meditators.[27] Additionally, each study adopted a distinct approach to testing FC. Whereas the three studies that found significant results all used whole-brain, seed-based FC, each chose a different seed (PCC only versus PCC and mPFC versus PCC and vmPFC). Furthermore, seed locations

[a]Seed-based FC describes an approach in which the time course of activation for a particular brain region, or "seed," is correlated with the activation time course from other regions of interest or individual voxels across the brain. The correlation between the seed time course and another region or voxel's time course provides a measure of FC. Seed-based FC approaches can therefore assess whether two particular regions tend to activate in synchrony and are often used in assessing brain networks.

[b]Brewer *et al.*[25] also failed to replicate this finding in their resting-state data, although they alternated between meditation and rest, possibly producing carryover effects that may have affected their ability to observe this effect.

Table 2. Within-network findings of significant FC relationships between network regions

Result	+/−	Mindfulness definition	Task	Method	*n*	Reference
Within default network						
Right PCC–vmPFC	+	MBSR training	Rest	PCC seed	14	76
Right PCC–dmPFC	+	MBSR training	Rest	PCC seed	14	76
Right PCC–left hippocampus	+	MBSR training	Rest	PCC seed	14	76
Left PCC/right PCC/ vmPFC–left vmPFC	+	More vs. less experienced experts	Rest	PCC/vmPFC seed	14	27
Right mPFC/ACC–left vmPFC	+	More vs. less experienced experts	Rest	mPFC/ACC seed	14	27
Right mPFC/ACC–right IPL	+	More vs. less experienced experts	Rest	mPFC/ACC seed	14	27
Right mPFC/ACC–left IPL	+	More vs. less experienced experts	Rest	mPFC/ACC seed	14	27
Right mPFC/ACC–left PCC	−	More vs. less experienced experts	Rest	mPFC/ACC seed	14	27
Left PCC–right PCC/precuneus	+	Experts vs. controls	Meditation (three types)	PCC seed	24	25
Left PCC–left cuneus/precuneus	+	Experts vs. controls	Meditation (three types)	PCC seed	24	25
Left PCC–left IPL/insula	+	Experts vs. controls	Meditation (three types)	PCC seed	24	25
Left mPFC–PHG	+	Experts vs. controls	Meditation (three types)	mPFC seed	24	25
Left PCC/Left mPFC–right (v)mPFC	+	Experts vs. controls	Rest	PCC/mPFC seed	68	77
DN (ACC/PCC)–DN (precuneus/cuneus)	−	Trait mindfulness (MAAS and FMI)	Rest	ICA	26	22
Right IPL–left dmPFC	+	Experts vs. beginners	Rest	Network analysis of nine DN seeds	23	26
Right IPL–right PCC/ precuneus	+	Experts vs. beginners	Rest	Network analysis	23	26
Right IPL–left IPL	+	Experts vs. beginners	Rest	Network analysis	23	26
Left vmPFC–left dmPFC	−	Experts vs. beginners	Rest	Network analysis	23	26
Left vmPFC–left PHG	−	Experts vs. beginners	Rest	Network analysis	23	26
Left IPL–left dmPFC	−	Experts vs. beginners	Rest	Network analysis	23	26
Left IPL–left PHG	−	Experts vs. beginners	Rest	Network analysis	23	26
Left IPL–right PHG	−	Experts vs. beginners	Rest	Network analysis	23	26
Left IPL–right PCC/ precuneus	−	Experts vs. beginners	Rest	Network analysis	23	26
Left dmPFC–left PHG	−	Experts vs. beginners	Rest	Network analysis	23	26
Left dmPFC–right PHG	−	Experts vs. beginners	Mindful breathing	dmPFC seed	31	92
Within executive network						
Right dPFC–left dlPFC	+	More vs. less experienced experts	Rest	dlPFC seed	14	27
Right dlPFC–right dlPFC	−	More vs. less experienced experts	Rest	dlPFC seed	14	27
Within salience network						
Right posterior insula–right anterior insula	+	MBSR training	Mindful breathing	Posterior insula seed	31	92

FC, functional connectivity; DN, default network; +/−, mindfulness-related increase or decrease in FC; mindfulness definition, operational definition of mindfulness; MBSR, mindfulness-based stress reduction; task, task performed while scanning; method, seed-based FC or ICA; ICA, independent component analysis.

Table 3. Between-network findings of significant FC relationships between network regions

Result	+/−	Mindfulness definition	Task	Method	*n*	Reference
Between default and salience						
Left PCC/right PCC/vmPFC–left ACC	−	More vs. less experienced experts	Rest	PCC/vmPFC seed	14	27
Left dACC/left insula/right insula–left IPL	+	More vs. less experienced experts	Rest	dACC/insula seed	14	27
Left PCC–right dACC	+	Experts vs. controls	Meditation (three types)	PCC seed	24	25
Left mPFC–left insula	+	Experts vs. controls	Meditation (three types)	mPFC seed	24	25
SN (insula)–posterior DN (PCC/precuneus)	−	Trait mindfulness (MAAS and FMI)	Rest	ICA	26	22
SN (insula)–anterior DN (ACC/PCC)	−	Trait mindfulness (MAAS and FMI)	Rest	ICA	26	22
SN (dACC)–dmPFC	+	MBSR training	Mindfulness of scanner	ICA	32	93
SN (sACC)–cuneus	−	MBSR training	Mindfulness of scanner	ICA	32	93
Left dmPFC–right insula	−	MBSR training	Mindful breathing	dmPFC seed	31	92
Right insula–left vmPFC	−	MBSR training (cross sectional)	Collapsed across tasks	Insula seed	36	78
Between executive and salience						
Right dlPFC–right insula	+	More vs. less experienced experts	Rest	dlPFC seed	14	27
Right insula–left dlPFC	+	MBSR training (cross sectional)	Collapsed across tasks	Insula seed	36	78
Between default and executive						
Left PCC–right dlPFC/left dlPFC	+	Experts vs. controls	Meditation (three types)	PCC seed	24	25
Right mPFC/ACC–right dlPFC	+	More vs. less experienced experts	Rest	mPFC/ACC seed	14	27
DN–EN	−	Zen experts vs. controls	Mindful breathing	ICA	24	79

FC, functional connectivity; DN, default network; EN, executive network; SN, salience network; +/−, mindfulness-related increase or decrease in FC; mindfulness definition, operational definition of mindfulness; MBSR, mindfulness-based stress reduction; task, task performed while scanning; method, seed-based FC or ICA; ICA, independent components analysis.

within common anatomical regions (i.e., the PCC) vary substantially. Table 4 provides the seed coordinates used in seed-based FC analyses across mindfulness studies and demonstrates the diversity of seed positions employed across studies; such diversity may contribute to the difficulty of finding direct replications across studies. The fourth study that did not fully replicate the result instead used independent component analysis to identify nine regions within the default network and examined the correlations between them. Despite this methodological diversity, a relatively consistent pattern of findings emerged between the PCC and the vmPFC.

Although this result is largely consistent, it is nevertheless somewhat difficult to interpret. This result is broadly consistent with what is known about subsystems of the default network. As described above, the PCC is part of a midline core subnetwork that shares reciprocal connections with the other subnetworks.[30,36] The PCC in particular demonstrates substantial FC with medial temporal regions of the default network,[50] which are part of the medial temporal subnetwork that includes the vmPFC. The increased FC between the PCC and the vmPFC therefore represents a strengthening of two regions that typically have high FC. The midline core of the default network is broadly associated with self-related processes and emotion/evaluation processes. Within this core system, the PCC has been linked to autonomic arousal and awareness and to monitoring for behaviorally relevant information.[47–49] The medial temporal

Table 4. Seed coordinates used in seed-based FC analyses across mindfulness studies

Seed description	Seed contributions	Approx. seed coordinates	Reference
Default network			
PCC	Left PCC	−8, −56, 26	25
PCC	Right PCC	8, −56, 30	76
PCC/vmPFC	Left PCC	−19, −60, 14	27
PCC/vmPFC	Right PCC	N/A	27
PCC/vmPFC	Right vmPFC	2, 37, −11	27
PCC/mPFC	Left PCC	−5, −49, 40	77
PCC/mPFC	Left mPFC	−1, 47, −4	77
mPFC	Left mPFC	−6, 52, −2	25
mPFC/ACC	Right mPFC/ACC	17, 58, −1	27
dmPFC	Left dmPFC	−10, 60, 22	26
dmPFC	Left dmPFC	−3, 27, 51	92
vmPFC	Left vmPFC	−2, 53, −9	26
IPL	Right IPL	47, −58, 27	26
IPL	Left IPL	−40, 70, 35	26
Executive network			
dlPFC	Right dlPFC	43, 31, 35	27
Salience network			
Right posterior insula–right anterior insula	Right posterior insula seed	39, −21, 21	92
dACC/INS	Left dACC	−10, 5, 33	27
dACC/INS	Left INS	−33, 24, −5	27
dACC/INS	Right INS	−40, 3, −6	27
Insula	Right INS	40, −8, 16	78

NOTE: Seed coordinates are listed in MNI 152 coordinate space and have been converted from other reported reference frames where necessary. In cases where seeds were produced from the combination of multiple distinct regional time courses, the location of each individual region is provided.

subsystem of the default network is associated with mental simulation, past- and future-oriented autobiographical thought, episodic memory, and contextual retrieval.[32,42,46] Increased FC between the PCC and vmPFC may therefore represent greater monitoring and evaluation of thought, though this interpretation remains speculative.

Other interpretations of this finding reflect the fact that the vmPFC region of the default network is also highly interconnected with salience network regions, such as the ACC and insula. Hasenkamp and Barsalou[27] have suggested that, because of this interconnectedness with salience network (and limbic) regions and association with viscera-motor processing, this increase in FC may provide default circuitry with greater access to information about internal states. Similarly, Jang *et al.*[77] have argued that this effect may reflect improved self-monitoring and the ability to inhibit irrelevant external and internal activity. It is possible that the shared connections between the vmPFC and salience network regions (the insula in particular) may be relevant in this regard, as improved vmPFC–PCC FC may heighten the ability of salience regions to effectively modulate default network activity.[27] This role of the salience network has been established,[55] and while Sridharan *et al.* did not find a direct causal link between insular cortex and vmPFC activity in their sample of meditation-naive individuals, they did observe that the insular cortex exerted a causal influence on PCC activity within these individuals; one possibility is thus that the interconnectedness of the vmPFC with salience network regions (despite its default network affiliation) provides an additional avenue through which the salience network can exert its influence on default network activity through mindfulness practice.

The second finding that shows some consistency across the literature is an increase in resting-state FC between regions of the salience and executive networks: the right-hemisphere insula (salience) and regions within the dlPFC (executive).[27,78] Hasenkamp and Barsalou compared resting-state FC among individuals who had either more than 2000 h of meditation practice or less than 1200 h of practice. Using a seed region within the right dlPFC, high-practice individuals had increased FC in several regions of the right insula.[27] Farb *et al.*[78] assessed the impact of a mindfulness-based stress reduction (MBSR) program on resting-state FC and obtained a similar result; however, they used the right insula as their seed region. Due to the central role the insula plays in interoception[70,71] and the dlPFC's involvement in executive processing, this finding has been interpreted to reflect greater access to present-moment and internal-state information represented within the insula when employing executive processing.[27] Farb *et al.*[78] also suggest that this increased FC relationship—when interpreted in the context of their other findings—reflects a shift toward more basic momentary self-reference, rather than the temporally extended form of narrative self-reference that may represent our default state. The insula receives moment-to-moment inputs from a variety of somatic and sensory systems, thereby storing a representation of one's state at each particular moment. The increased executive network integration with this information suggests the conscious processing of these aspects of momentary experience.

No other findings show a similar level of consistency across the literature. This is likely due to the diversity of methods employed, including various operational definitions of mindfulness (e.g., novices versus experts, various forms of mindfulness training, or dispositional levels of mindfulness), variation in tasks and/or task instructions, differing methods for analyzing FC, and variation in region-of-interest selection. It is worth noting that the effects that show some consistency have all been observed within resting-state scans, not mindfulness tasks themselves. It may be the case that brain function differs substantially across different forms of mindfulness tasks or practices, and that as a result it is implausible that consistency will be observed when comparing studies using different mindfulness tasks. In addition, each of these aforementioned sources of variance likely also contributes significantly to the apparent failure to conceptually replicate previous findings.

The inconsistency across findings that is typical for this literature is well illustrated by the three significant findings identified for FC between the default and executive networks. Whereas two studies found increased FC between the dlPFC and regions of the default network (PCC and mPFC/ACC, respectively), one study using independent component analysis found decreased FC between the entire default and executive networks.[25,27,79] These findings are not exact contradictions, but the pattern of both increased and decreased FC is difficult to reconcile. A likely explanation for this divergence is the diversity of methods employed. Each study used experts trained in a different contemplative tradition, thereby introducing variation in the specific mindfulness practices used to cultivate the expertise. Furthermore, each study used different scanning tasks and different FC methods and/or seeds. Given this variation, it is perhaps unsurprising that greater consistency has not emerged.

Although it is difficult to discern the signal from the noise across the existing set of findings, the results on the whole are generally not directly contradictory. It is possible that even if each study was rigorous and each finding was true, the conceptual integration across studies would still be limited by the diversity of methods, measures, and mindfulness practices involved. Like the parable of blind men each touching a different part of an elephant, the discrepancy in findings across studies may obscure a larger coherence or integration of findings that will emerge as research is able to better control for the multitude of factors involved in studying a construct as multifaceted as mindfulness to determine its neural basis in terms of interactions between dozens of relevant brain regions.

Although little consensus has yet emerged from the last 5 years of research into brain network interactions associated with mindfulness, the growing interest and rapid pace of innovation suggest that the next 5 years may usher in considerably greater clarity. Here, we highlight the best practices in intervention research and neuroimaging that in our view will be crucial to more efficiently advance this field.

Considerations for future research on mindfulness

Considerations for mindfulness interventions

The majority of neuroimaging research into mindfulness has compared experts—sometimes with more than 10,000 h of mindfulness practice—to either less-experienced experts, novices, or matched controls. While these studies have provided a valuable perspective, they have considerable limitations. Besides potential self-selection effects driven by individual differences that might lead someone to pursue expertise in mindfulness, experts are also exposed to a wide diversity of practices and worldviews throughout their training. This makes it impossible to discern which specific aspect of their training produces differences in brain network dynamics. Individual difference studies using mindfulness-naive participants avoid these issues but cannot characterize manifestations of mindfulness that require training. The greatest clarity of evidence will therefore come from randomized controlled trials that offer training to mindfulness-naive participants, and a number of methodological considerations can improve the interpretability of these studies.

Explicit operational definition of mindfulness

For research into mindfulness to meaningfully advance, researchers will need to carefully delineate their operational definition of mindfulness with respect to both its measurement and training. Existing classification schemes can assist in this effort.[80–82] For example, one scheme distinguishes between different families of meditation practices, including those that cultivate the self-regulation of attentional processes (the attentional family), those that cultivate cognitive and affective patterns that support well-being (the constructive family), and those that foster insight into the processes underlying perception, emotion, and cognition (the deconstructive family).[82] Another scheme characterizes mindfulness practices based on a phenomenological matrix with three orthogonal dimensions of subjective experience: (1) *object orientation*—the extent to which an experience or mental state is oriented toward some object or class of objects; (2) *dereification*—the degree to which thoughts, feelings, and perceptions are phenomenally interpreted as mental processes rather than as accurate depictions of reality object orientation; and (3) *meta-awareness*—the extent to which attention is directed toward explicitly noting the current contents of consciousness.[10] Although existing classification schemes can provide researchers with helpful guidance in describing their interventions, clarity and integration may only emerge when the field adopts a standardized instrument for characterizing a mindfulness intervention.

Selection of control

Using an adequate control group is essential in intervention research. Historically, many mindfulness interventions have utilized a no-control or wait-list control condition. Although a wait-list control can sometimes be the most appropriate design choice for certain research questions, both no-control and wait-list control conditions have limitations that need to be carefully considered. Without any control condition, no causal claims are merited. Improvements could result from test–retest effects (e.g., participants improve simply because of repeated exposure to testing material), self-selection effects (e.g., individuals who volunteered to participate were eager to change), regression to the mean effects (e.g., the tendency for a variable that is significantly different from the mean to return to the mean at other time points), maturation effects (e.g., the passing of time affecting participants such as getting older or becoming better educated), or history effects (e.g., influences external to the study, such as time of year).[83]

Wait-list control conditions can account for these effects. If a research question is best answered by controlling for only these effects, a wait-list control will be the most appropriate choice. However, precise causal or mechanistic claims are often limited by wait-list controls. For example, improvements may result from therapeutic alliance effects (e.g., the control group had no opportunity to interact with an interventionist), investment effects (e.g., the control group had less stake in the study and thus engaged with the testing materials differently than those with greater involvement), or placebo effects.[83] To merit causal claims that rule out these effects—as mindfulness research often aim to do—researchers generally need to adopt active controls.

In recent years, many mindfulness intervention studies have used active controls. Such control conditions are often intended to match the intervention on a number of therapeutic nonspecifics, such as the credibility and enthusiasm of the interventionist, the interpersonal experience of receiving an intervention, and the expectation of benefit. Although controlling for therapeutic nonspecifics can be important for many research questions, designing adequate active controls for multifaceted interventions, such as MBSR, can be challenging.

Specificity of intervention

Mindfulness interventions are often multifaceted. For example, MBSR involves several forms of meditation, yoga, small group discussion, class discussions facilitated by an instructor, and a broad curriculum that covers topics including stress physiology, stress reactivity, communication, attitudes, nonjudging, patience, trust, nonstriving, acceptance, and letting go.[84] Although multifaceted interventions play a crucial role in answering important questions about cognitive and neural plasticity, even modestly multifaceted interventions are constrained in their ability to determine the specific aspect of the intervention that alters cognitive processes or brain dynamics. This limitation is typically not addressed, even by the inclusion of an active control condition. Precise causal claims are only possible for a multifaceted intervention if the active control is also matched for all aspects of the intervention besides the single chosen element that is the focus of the investigation. In practice, this is rarely achieved. Even the Health Enhancement Program specifically designed to serve as an active control for MBSR cannot provide researchers with the ability to determine which of the various beliefs or mindfulness practices taught in MBSR are responsible for observed changes.[85] Effectively characterizing the neural correlates of mindfulness will benefit from more focused interventions, carefully matched controls, and/or mediational analyses.

Motivation, incentives, and expectations

Intervention research must also consider the effects of motivation to perform well on outcome measures and expectations for success. To minimize differences in pretest and posttest task motivation, financial incentives can be offered for objective task performance. This can help reduce the risk that those in the mindfulness condition show improved performance at posttesting due to enhanced motivation—for example, exerting more effort to focus their attention during a posttest mindfulness scan. In contrast, differential expectations for success need to be addressed on a study-by-study basis. Expectancy effects can produce spurious findings in some cases, while in others they serve as a mechanism underlying an intervention's effects. When an expectancy effect leads to a measured improvement that does not represent a true improvement in the underlying domain, it represents a spurious finding. In contrast, when an expectancy effect leads to improved performance on outcome measures that reflect genuine improvements in the underlying domain, then it acts as a mechanism. In this latter case, researchers must reflect carefully on whether the effects of expectations represent a confounder or a theoretically relevant mechanism with respect to their research question.

Intervention fidelity

Precisely defined mindfulness interventions not only produce more interpretable findings, but also allow for the more objective assessment of whether the intervention was delivered as intended—often described as *treatment fidelity* or *intervention fidelity*. Monitoring intervention fidelity helps ensure that participants receive the intended intervention without being introduced to any potentially confounding instructions or practices. Best practices for maintaining intervention fidelity include (1) delineating treatment definitions (e.g., specifications of features intended to be distinct and common across conditions), (2) formalizing treatment manuals (e.g., deciphering the stringency versus flexibility of an intervention protocol and the specificity versus abstractness of recommendations), and (3) verifying treatment integrity (e.g., recording interventions to be coded by hypothesis-blind raters for the presence or absence of treatment elements, potential confounds, and therapeutic nonspecifics).[86] Although treatment fidelity is fundamental to empirical testing of interventions, a 2007 analysis suggested that fewer than 2% of interventions adequately implemented treatment fidelity procedures.[87]

Considerations for neuroimaging research

In the rapidly evolving field of brain network science, many methodological considerations can advance neuroscientific investigation into mindfulness.

Better characterization of scanning tasks and experiences

Research into mindfulness has often involved scanning participants while they rest or while they complete a mindfulness exercise like attending to the sensations of their breath or the sound of the scanner. The basis of this approach assumes that individuals will vary in the mental states they experience during these scans, yet typically no attempt is made to characterize the nature of a participant's experience. Several laboratories are developing scales that provide retrospective reports of the content of thought during a task.[88] While practicing mindfulness, participants' attention will also inevitably fluctuate between different mental states, each possessing a unique neural basis. Mental state fluctuations during tasks have previously been assessed using experience-sampling methodologies,[27,34] yet such approaches impose additional task and response demands and are still limited in their ability to fully characterize the onset and offset of particular states. Dynamic FC analyses that use data-driven approaches to examine changes in patterns of FC throughout a scan may allow researchers to identify and characterize these discrete states rather than inadvertently collapsing across them.[89] These dynamic FC analyses are ushering in the increasingly realistic possibility of decoding complex patterns of neural activity into a characterization of the discrete mental states that are difficult to observe but nevertheless occur during neuroimaging scans. Finally, it is important that researchers recognize and account for potential carryover effects in the scanner, which could produce invalid results when mindfulness tasks are alternated with each other or with rest in relatively rapid sequence.

Accounting for imaging confounds

Functional magnetic resonance imaging is susceptible to the influence of a variety of physiological factors, including head motion, cardiac rate, and respiration rate.[90,91] In some cases, these factors can lead to spurious FC estimates. For instance, increased head motion can reduce the apparent FC between disparate brain regions while increasing FC estimates between nearby regions.[91] It is possible that more mindful individuals will tend to exhibit less head motion within the scanner, particularly during mindfulness tasks, and as such special care should be taken to account for possible differences in head motion during image preprocessing, as these differences may contribute to effects attributed to mindfulness practice. Similarly, cardiac and respiratory rates may differ systematically in more mindful individuals, especially during commonly assessed mindful breathing tasks, and should therefore also be considered in research design and analysis.

Assessing consistency of results across datasets

The paucity of direct replications across the existing neuroimaging literature on mindfulness, with regard to experimental designs, processing pipelines, and analysis methods, has limited the ability to draw reliable conclusions about the effects of mindfulness practice. However, sharing of datasets and/or reexaminations of datasets using analysis methods and processing pipelines from other published studies may provide an opportunity to test for the consistency of particular effects across datasets. While differences in subject groups, training approaches, and meditation instructions may magnify the noise in the data relative to the signal of each effect, reevaluations of results across studies using similar subject comparisons, training durations, or meditation instructions may allow for consistent effects to be observed that are not readily apparent from examinations of the published results within the current literature.

Summary and conclusions

Recent advances in neuroimaging and network science have provided new opportunities to examine the brain dynamics underlying the experience and training of mindfulness. Much of this work has focused on the default, executive, and salience networks given their respective roles in internal cognition, self-regulation, and awareness. An extensive review of this literature indicates that there is strikingly little consensus among existing research on mindfulness, although two of the most reliable findings appear to be (1) increased within-network FC between PCC and vmPFC default network regions and (2) increased between-network FC between the dlPFC (executive) and the insula (salience). The lack of convergence across results does not necessarily indicate that any of the existing findings are spurious because the substantial diversity in methods employed might obscure the integration of ultimately compatible results. By carefully taking stock of the many challenges that limit the integration of this literature, researchers can garner insights about how future work can more rapidly advance the field.

The challenges facing research into mindfulness bear some resemblance to the challenges an individual faces when first practicing mindfulness. One perspective on mindfulness suggests that it increases the ratio of signal to noise in our minds. By deliberately cultivating the faculty of attention, we become better able to direct our focus without getting carried away by the endless stream of internal and external distractions. Many claim that this ultimately allows one to see things more clearly—even to see things as they really are. Yet this achievement takes time and dedication. When someone first sets out to practice mindfulness, they typically discover that their minds are distracted by an overwhelming number of apparently random thoughts. Although this may feel like a problem—even an indication that the task is hopeless—mindfulness teachers often point out that it is actually a discovery. In taking stock of their minds, they gain appreciation for the work that will be required to develop mindfulness. Just as there are effective strategies for cultivating attention, there are methodological tools available to develop a stronger cognitive neuroscience of mindfulness. All of these strategies either increase signal or decrease noise, and together they may help us see the mindful brain as it really is.

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Conflicts of interest

The authors declare no conflicts of interest.

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