

The neuroscience of mindfulness meditation

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Abstract

Research over the past two decades broadly supports the claim that mindfulness meditation — practiced widely for the reduction of stress and promotion of health — exerts beneficial effects on physical and mental health, and cognitive performance. Recent neuroimaging studies have begun to uncover the brain areas and networks that mediate these positive effects. However, the underlying neural mechanisms remain unclear, and it is apparent that more methodologically rigorous studies are required if we are to gain a full understanding of the neuronal and molecular bases of the changes in the brain that accompany mindfulness meditation.

Main

Meditation can be defined as a form of mental training that aims to improve an individual's core psychological capacities, such as attentional and emotional self-regulation. Meditation encompasses a family of complex practices that include mindfulness meditation, mantra meditation, yoga, tai chi and chi gong¹. Of these practices, mindfulness meditation — often described as non-judgemental attention to present-moment experiences — has received most attention in neuroscience research over the past two decades^{2–8}.

Although meditation research is in its infancy, a number of studies have investigated changes in brain activation (at rest and during specific tasks) that are associated with the practice of, or that follow, training in mindfulness meditation. These studies have reported changes in multiple aspects of mental function in beginner and advanced meditators, healthy individuals and patient populations^{9–14}.

In this Review, we consider the current state of research on mindfulness meditation. We discuss the methodological challenges that the field faces and point to several shortcomings in existing studies. Taking into account some important theoretical considerations, we then discuss behavioural and neuroscientific findings in light of what we think are the core components of meditation practice: attention control, emotion regulation and self-awareness. Within this framework, we describe research that has revealed changes in behaviour, brain activity and brain structure following mindfulness meditation training. We discuss what has been learned so far from this research and suggest new research strategies for the field. We focus here on mindfulness meditation practices and have excluded studies on other types of meditation. However, it is important to note that other styles of meditation may operate via distinct neural mechanisms^{15,16}.

Challenges in meditation research

Findings on the effects of meditation on the brain are often reported enthusiastically by the media and used by clinicians and educators to inform their work. However, most of the findings have not yet been replicated. Many researchers are enthusiastic meditators themselves. Although their insider perspective may be valuable for a deep understanding of meditation, these researchers must ensure that they take a critical view of study outcomes. In fact, for meditation studies there is a relatively strong bias towards the publication of positive or significant results, as was shown in a meta-analysis¹⁷.

The methodological quality of many meditation research studies is still relatively low. Few are actively controlled longitudinal studies, and sample sizes are small. As is typical for a young research field, many experiments are not yet based on elaborated theories, and conclusions are often drawn from post-hoc interpretations. These conclusions therefore remain tentative, and studies must be carefully replicated. Meditation research also faces several specific methodological challenges.

Cross-sectional versus longitudinal studies. Early meditation studies were mostly cross-sectional studies: that is, they compared data from a group of meditators with data from a control group at one point in time. These studies investigated practitioners with hundreds or thousands of hours of meditation experience (such as Buddhist monks) and compared them with control groups of non-meditators matched on various dimensions^{9,18}. The rationale was that any effects of meditation would be most easily detectable in highly experienced practitioners.

A number of cross-sectional studies revealed differences in brain structure and function associated with meditation (see below). Although these differences may constitute training-induced effects, a cross-sectional study design precludes causal attribution: it is possible that there are pre-existing differences in the brains of meditators, which might be linked to their interest in meditation, personality or temperament^{2,19}. Although correlational studies have attempted to discover whether more meditation experience is related to larger changes in brain structure or function, such correlations still cannot prove that meditation practice has caused the changes because it is possible that individuals with these particular brain characteristics may be drawn to longer meditation practice.

More recent research has used longitudinal designs, which compare data from one or more groups at several time points and ideally include a (preferably active) control condition and random assignment to conditions^{11-14,20-25}. In meditation research, longitudinal studies are still relatively rare. Among those studies, some have investigated the effects of mindfulness training over just a few days, whereas others have investigated programmes of 1 to 3 months. Some of these studies have revealed changes in behaviour, brain structure and function^{11-14,20-25}. A lack of similar changes in the control group suggests that meditation has caused the observed changes, especially when other potentially confounding variables are controlled for properly²⁰⁻²².

Novice meditators versus expert meditators. Although most cross-sectional studies included long-term meditators^{9,17}, longitudinal studies are often conducted in beginners or naive subjects. Thus, differences in the results of cross-sectional and longitudinal analyses might be attributed to the different brain regions used during learning of meditation versus those used during the continued practice of an acquired skill. It would be interesting to follow subjects over a long-term period of practice to determine whether changes induced by meditation training persist in the absence of continued practice. However, such long-term longitudinal studies would be compromised by feasibility constraints, and it is likely that future longitudinal studies will remain restricted to relatively short training periods².

Control groups and interventions. It is important to control for variables that may be confounded with meditation training, such as changes in lifestyle and diet that might accompany the meditation practice or the expectancy and intention that meditation beginners bring to their practice. Researchers must carefully determine which variables are integral aspects of the meditation training and which can be controlled for. Some earlier studies only controlled for the length of time that the individual has practised meditation and the effects of repeated testing, but more recent studies have developed and included active interventions in control groups — such as stress management education²⁶, relaxation training^{14,23,27} or health enhancement programmes²⁰⁻²² — that can control for variables such as social interaction with the group and teachers, amount of home exercise, physical exercise and psychoeducation. These studies are therefore better able to extract and delineate the meditation-specific effects. For example, one study investigating short-term meditation training used a 'sham meditation' condition in which participants thought they were meditating, but did not receive proper meditation instructions, which allowed the researchers to control for factors such as expectancy, body posture and attention from the teacher²⁸. Mechanistic studies ideally need to use interventions that are as effective as mindfulness meditation in producing the beneficial effects on target variables but that allow for assessment of the unique mechanism underlying the mindfulness practice^{23,29}.

Control conditions in functional imaging. Although all functional neuroimaging studies must use appropriate comparison conditions, this challenge is particularly important when imaging meditative states. The comparison condition should be one in which a state of mindfulness meditation is not present. Many studies use resting comparison conditions, but a problem with this is that experienced practitioners are likely to enter into a state of meditation when at rest. However, other active tasks introduce additional brain activity that renders the comparison difficult to interpret. Using imaging protocols that do not rely on blood-oxygen-level-dependent contrasts (BOLD contrasts), such as arterial spin labelling, might be a possible solution for this problem³⁰.

Mindfulness and emotion regulation

Enhanced emotion regulation has been suggested to underlie many of the beneficial effects of mindfulness meditation. Emotion regulation refers to strategies that can influence which emotions arise and when, how long they occur, and how these emotions are experienced and expressed. A range of implicit and explicit emotion regulation processes has been proposed⁸⁶, and mindfulness-based emotion regulation may involve a mix of these processes, including attentional deployment (attending to mental processes, including emotions), cognitive change (altering typical patterns of appraisal regarding one's emotions) and response modulation (decreasing tonic levels of suppression).

Effects of mindfulness meditation on emotion regulation. Improvements in emotion regulation associated with mindfulness meditation have been investigated through various approaches, including experimental studies, self-reporting studies, measurement of peripheral physiology and neuroimaging¹⁰. These studies have reported various positive effects of mindfulness meditation on emotional processing, such as a reduction in emotional interference by unpleasant stimuli⁸⁷, decreased physiological reactivity and facilitated return to emotional baseline after response to a stressor film⁸⁸, and decreased self-reported difficulties in emotion regulation⁸⁹. Consequently, lowered intensity and frequency of negative affect^{90,91} and improved positive mood states^{14,91,92} are reported to be associated with mindfulness meditation.

Neural mechanisms of improved emotion regulation. Neuroimaging studies that have probed the enhanced emotion regulation associated with mindfulness meditation in an attempt to identify the underlying brain activation patterns typically present study participants with emotional pictures^{82,93-97}, words and/or statements^{29,98} and instruct them to encounter these with a state of mindfulness or a simple baseline state.

The hypothesis that drives many of these studies is that mindful emotion regulation works by strengthening prefrontal cognitive control mechanisms and thus downregulates activity in regions relevant to affect processing, such as the amygdala. Present-moment awareness and non-judgemental acceptance through mindfulness meditation^{8,10} are thought to be crucial in promoting cognitive control because they increase sensitivity to affective cues that help to signal the need for control⁹⁹. Studies have therefore investigated whether mindfulness training exerts its effects through enhanced top-down control or facilitated bottom-up processing¹⁰⁰. The findings (outlined below) suggest that the level of expertise is important, with beginners showing a different pattern from expert meditators. However, although several studies have pointed to the involvement of fronto-limbic regions, very few studies have begun to relate changes in these regions to changes in measures of behaviour or well-being¹⁰.

A frequently reported finding is that mindfulness practice leads to (or is associated with) a diminished activation of the amygdala in response to emotional stimuli during mindful states^{83,94,95} as well as in a resting state⁹³, suggesting a decrease in emotional arousal. However, although such results have been reported for meditation beginners, they have less consistently been detected in experienced meditators⁹⁵ (but see Ref. 18).

Prefrontal activations are often enhanced as an effect of mindfulness meditation in novice meditators (but see Ref. 29): for example, greater dorsolateral PFC responses were found during executive processing within an emotional Stroop task in healthy individuals after 6 weeks of mindfulness training⁸². Enhanced dorsomedial and dorsolateral PFC activation was also detected when participants expected to see negative images while engaging in a mindful state⁹⁴. Moreover, after an MBSR course, an enhanced activation in the ventrolateral PFC in people suffering from anxiety was found when they labelled the affect of emotional images⁹⁷. By contrast, experienced meditators have been found to show diminished activation in medial PFC regions⁹⁵. This finding could be interpreted as indicating reduced control (disengagement of elaboration and appraisal) and greater acceptance of affective states.

Neuroimaging studies of ameliorated pain processing through mindfulness meditation have also pointed to expertise-related differences in the extent of cognitive control over sensory experience. Meditation beginners showed increased activity in areas involved in the cognitive regulation of nociceptive processing (the ACC and anterior insula) and areas involved in reframing the evaluation of stimuli (the orbitofrontal cortex), along with reduced activation in the primary somatosensory cortex in a 4-day longitudinal study with no control group³⁰, whereas meditation experts were characterized by decreased activation in dorsolateral and ventrolateral PFC regions and enhancements in primary pain processing regions (the insula, somatosensory cortex and thalamus) compared with controls in two cross-sectional studies^{35,81}.

These findings are in line with the assumption that the process of mindfulness meditation is characterized as an active cognitive regulation in meditation beginners, who need to overcome habitual ways of internally reacting to

one's emotions and might therefore show greater prefrontal activation. Expert meditators might not use this prefrontal control. Rather, they might have automated an accepting stance towards their experience and thus no longer engage in top-down control efforts but instead show enhanced bottom-up processing¹⁰⁰.

In the early stages of meditation training, achieving the meditation state seems to involve the use of attentional control and mental effort; thus, areas of the lateral prefrontal and parietal cortex are more active than before training^{11,16,100,101}. This may reflect the higher level of effort often found when participants struggle to obtain the meditation state in the early stages^{11,73,98,102}. However, in the advanced stages, prefrontal–parietal activity is often reduced or eliminated, but ACC, striatum and insula activity remains^{9,10,53,73,76,101–103}. Whether effort has a key role in PFC and ACC activation during or following meditation needs further investigation.

Analysis of functional connectivity between regions of the fronto-limbic network could help to further elucidate the regulatory function of executive control regions. Only a few studies have included such analyses. One cross-sectional study on pain processing in meditators demonstrated decreased connectivity of executive and pain-related brain regions³⁵, and one study of mindfulness-naïve smokers demonstrated reduced connectivity between craving-related brain regions during a mindfulness condition compared to passive viewing of smoking-related images during cigarette craving⁹⁶, suggesting a functional decoupling of involved regions. Another longitudinal, randomized study reported that people suffering from anxiety showed a change from a negative correlation between the activity of frontal regions and that of the amygdala before intervention (that is, negative connectivity) to a positive correlation between the activity of these regions (positive connectivity) after a mindfulness intervention⁹⁷. Because such a negative correlation will occur when prefrontal regions downregulate limbic activation^{104,105}, it was speculated that the positive coupling between the activity of the two regions after mindfulness intervention might indicate that meditation involves monitoring of arousal rather than a downregulation or suppression of emotional responses, and that it might be a unique signature of mindful emotion regulation. Importantly, this study also investigated the correlation between neural and self-reported findings and demonstrated that the changes in PFC–amygdala connectivity were correlated with anxiety symptom improvement. Further studies are needed to elucidate the complex interplay between regions of the fronto-limbic network in mindfulness meditation.

Although the proposed similarities between mindfulness and the reappraisal strategy of emotion regulation have been much debated, there is some evidence that mindfulness also shares similarities with extinction processes.

Brain regions involved in motivation and reward processing also show functional alterations that are related to mindfulness training, such as stronger activity of the putamen and caudate during a resting state following mindfulness training²³ and lower activation in the caudate nucleus during reward anticipation in experienced meditators¹⁰⁶. These studies might indicate altered self-regulation in the motivational realm, with possibly reduced susceptibility to incentives and enhanced reward-related activity during rest.

Brain regions involved in the regulation of emotions have also shown structural changes following mindfulness meditation^{31,32,38–41,48,51}. Although these findings provide some initial evidence that these brain regions are related to mindfulness practice, the question of whether they are involved in mediating the beneficial effects of mindfulness meditation remains largely unanswered.

Mindfulness and self-awareness

According to Buddhist philosophy, the identification with a static concept of 'self' causes psychological distress. Dis-identification from such a static self-concept results in the freedom to experience a more genuine way of being. Through enhanced meta-awareness (making awareness itself an object of attention), mindfulness meditation is thought to facilitate a detachment from identification with the self as a static entity^{3,10,107} and a tendency to identify with the phenomenon of 'experiencing' itself is said to emerge^{15,108–112}. Currently, empirical research into this area is only just emerging^{111,113}, and the few interpretations of connections between neuroimaging findings and self-reported data — which we will summarize briefly below — are suggestive at best.

Self-referential processing. Altered self-representation has been investigated with questionnaire studies. Early studies reported mindfulness training to be associated with a more positive self-representation, higher self-esteem, higher acceptance of oneself¹¹⁴ and styles of self-concept that are typically associated with less-severe pathological symptoms¹¹⁵. Meditators have also been shown to score higher than non-meditators on a scale that measures

non-attachment¹¹⁶: a construct that is based on insight into the constructed and impermanent nature of mental representations. Although such concepts are not easy to capture in experimental and neuroscientific studies, findings from a few recent studies seem to suggest that brain structures supporting self-referential processing might be affected by mindfulness meditation^{98,117,118}.

Although there is much debate about its exact function, a widespread view holds that the default mode network (DMN)^{119,120} is involved in self-referential processing. This network includes midline structures of the brain, such as areas of the medial PFC, posterior cingulate cortex (PCC), anterior precuneus and inferior parietal lobule^{121,122}. These structures show high activity during rest, mind wandering and conditions of stimulus-independent thought¹²¹ and have been suggested to support diverse mechanisms by which an individual can 'project' themselves into another perspective¹²³. fMRI studies have investigated activity in the DMN in association with mindfulness practice. Regions of the DMN (the medial PFC and PCC) showed relatively little activity in meditators compared to controls across different types of meditation, which has been interpreted as indicating diminished self-referential processing¹¹⁷. Functional connectivity analysis revealed stronger coupling in experienced meditators between the PCC, dorsal ACC and dorsolateral PFC, both at baseline and during meditation, which was interpreted as indicating increased cognitive control over the function of the DMN¹¹⁷. Increased functional connectivity was also found between DMN regions and the ventromedial PFC in participants with more compared to less meditation experience¹¹⁸. It has been speculated that this increased connectivity with ventromedial PFC regions supports greater access of the default circuitry to information about internal states because this region is highly interconnected with limbic regions¹¹⁸.

Awareness of present-moment experiences. Evaluative self-referential processing is assumed to decrease as an effect of mindfulness meditation, whereas awareness of present-moment experiences is thought to be enhanced. Mindfulness practitioners often report that the practice of attending to present-moment body sensations results in an enhanced awareness of bodily states and greater perceptual clarity of subtle interoception. Empirical findings to support this claim are mixed. Although studies that assessed performance on a heartbeat detection task — a standard measure of interoceptive awareness — found no evidence that meditators had superior performance to non-meditators^{124,125}, other studies found that meditators showed greater coherence between objective physiological data and their subjective experience in regard to an emotional experience¹²⁶ and the sensitivity of body regions¹²⁷.

Multiple studies have shown the insula to be implicated in mindfulness meditation: it shows stronger activation during compassion meditation¹²⁸ and following mindfulness training^{23,52,98}, and has greater cortical thickness in experienced meditators³². Given its known role in awareness¹²⁹, it is conceivable that enhanced insula activity in meditators might represent the amplified awareness of present-moment experience.

Similarly, a study reported an uncoupling of the right insula and medial PFC and increased connectivity of the right insula with dorsolateral PFC regions in individuals after mindfulness training⁹⁸. The authors interpret their findings as a shift in self-referential processing towards a more self-detached and objective analysis of interoceptive and exteroceptive sensory events, rather than their affective or subjective self-referential value. Furthermore, a preliminary analysis from a study of a state of 'non-dual awareness' (a state of awareness in which perceived dualities, such as the distinction between subject and object, are absent) showed a decreased functional connectivity of the central precuneus with the dorsolateral PFC. The author speculates that this finding might be indicative of a state in which awareness is itself the subject of awareness¹¹¹.

Together, the findings from these studies have been taken to suggest that mindfulness meditation might alter the self-referential mode so that a previous narrative, evaluative form of self-referential processing is replaced by greater awareness^{98,111}. We suggest that this shift in self-awareness is one of the major active mechanisms of the beneficial effects of mindfulness meditation. However, because these interpretations are built on a still-fragmentary understanding of the function of the involved brain regions, future research will need to test and elaborate these assumptions.

Across the functional and structural MRI studies that have been published to date, especially those based on the longitudinal, randomized, controlled studies with active control groups and meta-analyses, the ACC, PFC, PCC, insula, striatum (caudate and putamen) and amygdala seem to show consistent changes associated with mindfulness meditation^{9-11,13,17,23,34,73,108,130} (Table 1). We consider these areas to be the core regions involved in self-regulation of attention, emotion and awareness following mindfulness training. However, we acknowledge that

many other brain areas are also involved in mindfulness practice and warrant further investigation using rigorous randomized and controlled designs.

Table 1 Evidence for changes in the core brain regions after mindfulness meditation

Brain region	Study design	Findings*	Refs
ACC (self-regulation of attention and emotion)	Cross-sectional, Vipassana meditators (N = 15) versus controls (N = 15)	Enhanced ACC activation during breath awareness (focused attention) meditation	76
	Longitudinal, IBMT versus active control (relaxation training) (N = 23 each group)	Enhanced ACC activity in resting state	23
PFC (attention and emotion)	Longitudinal, mindfulness training (N = 30) versus active control (N = 31)	Greater dorsolateral PFC activation during emotional Stroop executive processing	82
	Longitudinal, patients with generalized anxiety disorder, MBSR (N = 15) versus active control (N = 11)	Enhanced activation of ventrolateral PFC, enhanced connectivity of several PFC regions with amygdala	97
	Longitudinal, uncontrolled, before and after mindfulness training (N = 15)	Anxiety relief following mindfulness training was related to ventromedial PFC and ACC activation (along with insula)	157
PCC (self-awareness)	Cross-sectional, expert meditators (N = 12) versus controls (N = 13)	PCC deactivation during different types of meditation, increased coupling with ACC and dorsolateral PFC	117
	Cross-sectional, expert meditators (N = 14) divided into high and low practice groups	Reduced connectivity between left PCC and medial PFC and ACC at rest in high practice group	118
	Longitudinal, IBMT, active control (relaxation training) (N = 23 each group)	Enhanced right PCC activity at resting state	23
Insula (awareness and emotional processing)	Cross-sectional, MBSR (N = 20) and waiting list control (N = 16)	Greater anterior insula activation and altered coupling between dorsomedial PFC and posterior insula during interoceptive attention to respiratory sensations	52
	Cross-sectional, expert Tibetan Buddhist meditators (N = 15) and novices (N = 15)	Enhanced insula activation when presented with emotional sounds during compassion meditation	128
	Longitudinal, IBMT, active control (relaxation training) (N = 23 each group)	Enhanced left insula activity at resting state	23
Striatum (regulation of attention and emotion)	Longitudinal, IBMT, active control (relaxation training) (N = 23 each group)	Enhanced caudate and putamen activity at resting state	23
	Cross-sectional, expert meditators (N = 34) and controls (N = 44)	Lower activation in the caudate nucleus during reward anticipation	106
Amygdala (emotional processing)	Longitudinal, mindful attention training (N = 12), compassion training (N = 12) and active control (N = 12)	Decreased activation in right amygdala in response to emotional pictures in a non-meditative state	93
	Longitudinal, uncontrolled, patients with social anxiety disorder before and after MBSR (N = 14)	Diminished right dorsal amygdala activity during reacting to negative self-belief statements	83
	Cross-sectional, beginner (N = 10) and expert Zen meditators (N = 12)	Downregulation of the left amygdala when viewing emotional pictures in a mindful state in beginner but not expert meditators	95

Exemplary studies for each region support its involvement in mindfulness (the list is not comprehensive). Future research will need to test the hypothesized functions by relating behavioural and neuroimaging findings. ACC, anterior cingulate cortex; IBMT, integrative body–mind training; MBSR, mindfulness-based stress reduction; PCC, posterior cingulate cortex; PFC, prefrontal cortex. *Meditators show increased values, unless otherwise noted.

Future questions

Mechanisms of mindfulness-induced changes. A number of studies seem to suggest that mindfulness meditation induces changes in brain structure and function, raising the question of which underlying mechanisms support these processes. It is possible that engaging the brain in mindfulness affects brain structure by inducing dendritic branching, synaptogenesis, myelinogenesis or even adult neurogenesis. Alternatively, it is possible that mindfulness positively affects autonomic regulation and immune activity, which may result in neuronal preservation, restoration and/or inhibition of apoptosis^{14,23,131}. It is well known that mindfulness-based techniques are highly effective in stress reduction, and it is possible that such stress reduction may mediate changes in brain function^{14,48,132–137}. A combination of all of these mechanisms may even occur.

It is also important to realize that the direction of the observed effects of mindfulness meditation has not been consistent across all studies. Although larger values in meditators compared to controls are predominantly reported, a cross-sectional study also revealed smaller fractional anisotropy and cortical thickness values in meditators in some brain regions, including the medial PFC, postcentral and inferior parietal cortices, PCC and medial occipital cortex¹³⁸. Along these lines, mindfulness-induced increases are predominantly observed in longitudinal studies. However, it was also reported, for example, that as a consequence of meditation, larger decreases in perceived stress were associated with larger decreases in grey-matter density in the amygdala⁴⁸.

Thus, the underlying mechanisms seem to be more complex than currently assumed, and further research is necessary.

Although neuroimaging has advanced our understanding of the individual brain regions involved in mindfulness meditation, most evidence supports the idea that the brain processes information through the dynamic interactions of distributed areas operating in large-scale networks^{139,140}. Because the complex mental state of mindfulness is probably supported by alterations in large-scale brain networks, future work should consider the inclusion of complex network analyses, rather than restricting analyses to comparisons of the strength of activations in single brain areas. Recent studies have explored functional network architecture during the resting state using these new tools^{141,142}.

Decoding mental states. Mindfulness meditation approaches can be divided into those involving focused attention and those involving open monitoring. Even within the same meditation style, practitioners can be at different stages of mindfulness practice². Investigating the distinction between these different stages in terms of brain function will require new advanced tools and methods. For instance, simultaneous multi-level recording — using fMRI and electrophysiology — could provide information on how the brain and body interact to support the meditation practice¹⁴³. Electroencephalography feedback has been used to aid training and study meditation by providing the practitioners with information on the brain waves they are producing. Similarly, real-time fMRI has been used to provide subjects with feedback of the brain activity they are producing and allows the experimenter to examine pain, cognitive control, emotion regulation and learning of meditation. This dynamic recording and feedback technique may help to train the subjects effectively and allow their mental states at different stages of mindfulness training to be decoded from their brain activity^{144–146}, possibly by applying techniques such as multivariate pattern analysis¹⁴⁷.

Interpretations of study outcomes remain tentative until they are clearly linked to subjective reports or behavioural findings. Future studies should therefore increasingly draw connections between behavioural outcomes and neuroimaging data using the advanced multi-level analyses mentioned above.

Investigating individual differences. People respond to mindfulness meditation differently. These differences may derive from temperamental, personality or genetic differences. Studies in other fields have suggested that genetic polymorphisms may interact with experience to influence the success of training¹⁴⁸. Because mindfulness meditation affects the activation and connectivity of the ACC, PFC and other brain regions involved in cognitive control and emotion regulation, it might be helpful to examine these polymorphisms to determine their possible influence on the success of meditation practice^{2,59,149}. Moreover, individual differences in personality, lifestyle, life events and trainer–trainee dynamics are likely to have substantial influence on training effects, although little is known about these influences. Mood and personality have been used to predict individual variation in the improvement of creative performance following mindfulness meditation¹⁵⁰. Capturing temperament and personality differences may serve to predict success in mindfulness training^{150,151} because different temperament and personality traits are reported to be associated with different electroencephalography patterns and heart-rate variability in Zen meditators¹⁵².

Clinical application. Self-regulation deficits are associated with diverse behavioural problems and mental disorders, such as increased risk of school failure, attention deficit disorder, anxiety, depression and drug abuse^{78,153}. Convergent findings indicate that mindfulness meditation could ameliorate negative outcomes resulting from deficits in self-regulation and could consequently help patient populations suffering from diseases and behavioural abnormalities. Several clinical trials have explored the effects of mindfulness meditation on disorders such as depression¹⁵⁴, generalized anxiety²⁶, addictions¹⁵⁵, attention deficit disorders¹⁵⁶ and others⁴², and have begun to establish the efficiency of mindfulness practice for these conditions. Only a few recent studies, however, have investigated the neuroplastic changes underlying these beneficial effects of mindfulness in clinical populations^{29,41,42,74,97,142,157}. Although these studies are promising, future work needs to replicate and expand the emerging findings to optimally tailor interventions for clinical application.

Conclusions

Interest in the psychological and neuroscientific investigation of mindfulness meditation has increased markedly over the past two decades. As is relatively common in a new field of research, studies suffer from low methodological quality and present with speculative post-hoc interpretations. Knowledge of the mechanisms that

underlie the effects of meditation is therefore still in its infancy. However, there is emerging evidence that mindfulness meditation might cause neuroplastic changes in the structure and function of brain regions involved in regulation of attention, emotion and self-awareness. Further research needs to use longitudinal, randomized and actively controlled research designs and larger sample sizes to advance the understanding of the mechanisms of mindfulness meditation in regard to the interactions of complex brain networks, and needs to connect neuroscientific findings with behavioural data. If supported by rigorous research studies, the practice of mindfulness meditation might be promising for the treatment of clinical disorders and might facilitate the cultivation of a healthy mind and increased well-being.

Glossary

Longitudinal studies: Study designs that compare data from one or more groups at several time points and that ideally include a (preferably active) control condition and random assignment to conditions.

Cross-sectional studies: Study designs that compare data from an experimental group with those from a control group at one point in time.

Correlational studies: Studies that assess the co-variation between two variables: for example, co-variation of functional or structural properties of the brain and a behavioural variable, such as reported stress.

Blood-oxygen-level-dependent contrasts: (BOLD contrasts). Signals that can be extracted with functional MRI and that reflect the change in the amount of deoxyhaemoglobin that is induced by changes in the activity of neurons and their synapses in a region of the brain. The signals thus reflect the activity in a local brain region.

Arterial spin labelling: (ASL). An MRI technique that is capable of measuring cerebral blood flow in vivo. It provides cerebral perfusion maps without requiring the administration of a contrast agent or the use of ionizing radiation because it uses magnetically labelled endogenous blood water as a freely diffusible tracer.

Brain state: The reliable patterns of brain activity that involve the activation and/or connectivity of multiple large-scale brain networks.

Fractional anisotropy: A parameter in diffusion tensor imaging, which images brain structures by measuring the diffusion properties of water molecules. It provides information about the microstructural integrity of white matter.

Axial and radial diffusivity: Derived from the eigenvalues of the diffusion tensor, their underlying biophysical properties are associated with axonal density and myelination, respectively.

Activation likelihood estimation meta-analysis: A technique for coordinate-based meta-analysis of neuroimaging data. It determines the convergence of foci reported from different experiments, weighted by the number of participants in each study.

Multivariate pattern analysis: A method of analysing functional MRI data that is capable of detecting and characterizing information represented in patterns of activity distributed within and across multiple regions of the brain. Unlike univariate approaches, which only identify magnitudes of activity in localized parts of the brain, this approach can monitor multiple areas at once.