For thousands of years, contemplatives have reported that enhancements in sensory awareness, cognition, and health can be accomplished through meditation practice. Before the development and utilization of neuroimaging and other scientific methodologies, the scientific world cast these descriptions as reflections of a relaxation response at best, and report biases associated with practitioner zeal at worst. The recent surge in number of mindfulness-based studies has supported the claim that mindfulness meditation can improve a range of mental and physical health outcomes, and neuroimaging studies are beginning to identify the brain mechanisms that mediate the relationships between mindfulness meditation and such outcomes. Although the neuroscientific investigation of mindfulness meditation is in its infancy, the premise of this chapter is that mindfulness meditation engages a unique, distributed network of brain regions.

Recent accounts of mindfulness meditation have delineated some of the psycho-neurobiological mechanisms of action of this method of mental training (Austin, 1998; Cahn & Polich, 2006; Hölzel et al., 2011) and offered theoretical frameworks to describe and explain meditation-based changes in neurocognitive and self-related processes (Vago & Silbersweig, 2012). However, discrepancies between meditation traditions, and differing characteristics and durations of training highlight the importance of delineating the neurobiological mechanisms of mindfulness meditation from a longitudinal perspective. Therefore, a comprehensive description of the brain mechanisms supporting mindfulness meditation must consider commonalities and differences across training levels. This chapter builds on previous neuroscientific work by offering a complementary perspective that focuses on a temporal account of the neurobiology of mindfulness, which considers the neurobiological basis of how
mindfulness engages the brain over time. In this chapter, I first provide a brief overview describing some key neuroimaging methodologies used in research. In the sections to follow, I provide a descriptive account of the neurobiological correlates of dispositional mindfulness, brief meditation training (1 week or less), the mindfulness-based stress reduction (MBSR) program (approximately 8 weeks), and finally expert meditators (more than 1,000 hours of practice). The subsequent section, concerning mindfulness and the default mode network, briefly describes how different levels of mindfulness-related experience affect task-independent neural processing. I then provide a longitudinal perspective of the brain structural correlates associated with different levels of mindfulness. Finally, I discuss considerations for future mindfulness-based and other contemplative practice research.

A Stage-Based Account of the Neurobiology of Mindfulness Meditation

In this chapter, I argue that the neurobiology of mindfulness varies across different levels of meditation training (Figure 10.1). The proposed neurobiological model of mindfulness meditation is quite consistent with and based on the underlying principles of mindfulness postulated to develop across varying levels of proficiency in different meditative practice traditions (Gunaratana, 2002; Lutz, Slagter, Dunne, & Davidson, 2008; Wallace, 2006). I propose that mindfulness meditation is associated with higher-order brain mechanisms such as the prefrontal cortex (PFC) and the anterior cingulate cortex (ACC) at early stages of this form of mental training. This pattern of neural activity is also evident in those who have never meditated, but whose reports indicate higher levels of trait mindfulness. Because some accounts of mindfulness meditation are based on attending to arising sensory events, sensory appraisal-based brain regions such as the anterior insula and the somatosensory cortices are activated across all meditation training levels. However, at early stages of mindfulness meditation training and development, practitioners engage brain mechanisms supporting an effortful top-down regulation of lower-level afferent processing, indicated by greater activation in the PFC and ACC and deactivation of the thalamus and the amygdala, brain regions involved in early stages of sensory and emotional processing, respectively. As the meditator becomes more skilled at attending to sensory and emotional experiences without interpretation or elaboration, a decoupling between brain mechanisms supporting appraisals of sensory processing develops, as indicated by decreases in higher-order brain activity (PFC) and increases in sensory-processing brain regions (anterior insula, somatosensory cortices). I also postulate that robust changes in brain structure are associated with extensive training in mindfulness meditation and higher levels of dispositional mindfulness. Some initial studies suggest that mindfulness meditation can offset and/or buffer against age-related cortical thinning (Grant, Courtemanche, Duerden, Duncan, & Rainville, 2010; Hölzel et al., 2008; Lazar et al., 2005). In fact, adept meditation practitioners exhibit significant reductions in neural structures associated with emotional processing (amygdala) and increased thickness in brain regions associated with sensory awareness (insula). These findings suggest that long-term training in mindfulness meditation
The Neurobiology of Mindfulness Meditation

<table>
<thead>
<tr>
<th>Behavioral mechanisms</th>
<th>Brain mechanisms</th>
</tr>
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</table>
| **Trait mindfulness** | • Labeling emotions as they arise  
  • Cognitive reappraisal  
  • Reduced mind-wandering |
| **Brief meditation training (<1 week)** | • Cognitive reappraisal  
  • Reduced mind wandering  
  • Interoceptive awareness  
  • Reward processing |
| **MBSR (8 weeks): State effects** | • Interoceptive awareness  
  • Sensory evaluation  
  • Cognitive control |
| **MBSR (8 weeks): Trait effects** | • Interoceptive awareness  
  • Working memory  
  • Cognitive control of emotion |
| **Expert meditators (>1,000 hours of meditation training)** | • Interoceptive awareness  
  • Cognitive control of emotion  
  • Sensory evaluation  
  • Reward Processing  
  • Reduced mind-wandering |
| **Expert meditators (>1,000 hours of training): Trait effects** | • Higher sensory processing  
  • Reduced evaluation/appraisals  
  • Reduced mind-wandering  
  • Interoceptive awareness |

**FIGURE 10.1.** Current understanding of the neurobiology of mindfulness meditation. *First row:* Trait mindfulness has been associated with cognitive reappraisal processes and interoceptive awareness. The neural correlates of these behavioral outcomes are reflected in down-regulation of the amygdala by the prefrontal cortex (PFC) as well as reduced default-mode network activation. *Second row:* Meditating after brief meditation training engages brain mechanisms supporting reduced mind wandering (default-mode network) and amygdala activation (emotional processing), and greater activation in brain regions involved in reward processing (orbitofrontal cortex [OFC]), cognitive control and emotion regulation (OFC, rostral anterior cingulate cortex [rACC], perigenual ACC [pgACC]), sensory evaluation (secondary somatosensory cortices [S2]), and interoceptive awareness (right anterior insula). *Third row:* After training in mindfulness-based stress reduction (MBSR) programs, meditation produces brain activation in the PFC (cognitive control), right anterior insula (interoceptive awareness), and S2 (sensory evaluation). Stabilized, trait-like effects associated with MBSR (*fourth row*) are associated with reducing structural gray-matter density in the amygdala (emotional processing), and increasing gray-matter density in the hippocampus (working memory), temporoparietal junction (TPJ), and posterior cingulate cortex (PCC), brain regions associated with self-referential processes. Adept meditators show activation in the rACC, right anterior insula, putamen, and PFC during meditation (*fifth row*) and deactivation in the default mode brain network. Long-term changes in expert meditators (*sixth row*) are reflected by increases in gray matter and regional blood signals in sensory processing brain regions (S2, thalamus, posterior insula), and reduced activation in higher-order evaluative neural regions (PFC) and the default mode network.
may produce stabilized, “plastic” changes that can potentially support mindfulness-related enhancements in cognition and health. Taken together, the proposed model (Figure 10.1) provides an initial neurobiological account for the ways in which mindfulness meditation differentially engages a unique set of brain regions across different stages of meditative training. Before turning to the evidence for this model, I first briefly describe the neuroscientific methods used in mindfulness meditation-related research (for more, see He, Yang, Wilke, & Yuan, 2011; Howseman & Bowtell, 1999; Tang & Posner, Chapter 5, this volume).

**Overview of Neurophysiological Methodologies**

Mindfulness-based neuroscience has used two primary neurophysiological methods to identify the brain mechanisms associated with meditation. First, electroencephalography (EEG) uses electrodes placed on the scalp to record activity of electrical currents produced by neural synaptic activity. The event-related potential (ERP) is a neural marker embedded within continuous EEG signals that corresponds to a singular (predetermined) external event (i.e., attending to an exogenously driven stimulus). Although the spatial resolution of EEG/ERP is not very high, it is suitable for capturing when a cognitive and/or sensory event occurs; that is, it has high temporal resolution, on the order of milliseconds.

The development of neuroimaging methods, such as functional magnetic resonance imaging (fMRI), positron emission tomography (PET), and arterial spin labeling (ASL) fMRI, has provided means to collect direct (perfusion-based fMRI; PET) and indirect (blood oxygen level-dependent [BOLD]; fMRI) measures of cerebral blood flow (CBF), which provide higher spatial resolution (i.e., indicating where neural activity may be occurring), although this comes at a tradeoff, with poorer temporal resolution (2–5 seconds) than EEG/ERP.

**Neural Correlates of Dispositional Mindfulness**

Although the focus of this chapter is on delineation of the neural mechanisms supporting the effects of mindfulness meditation across different mental training levels, it is important to recognize that self-reported dispositional mindfulness is also associated with engaging a unique set of brain mechanisms. In the research community, dispositional mindfulness is measured in a basic way and is typically considered an inherent ability to sustain nonevaluative attention and/or receptive awareness to ongoing events and experiences. Not surprisingly, there is considerable interindividual variability in this capacity, and such differences have been associated with mindfulness theory-consistent neurobiological and other outcomes. For example, individuals reporting higher levels of dispositional mindfulness exhibit reduced neuroendocrine stress reactivity (Brown, Weinstein, & Creswell, 2012; Ciesla, Reilly, Dickson, Emanuel, & Updegraff, 2012; Tamagawa et al., 2013), lower amygdala activity at rest (opposed to those reporting higher depressive symptoms) (Way, Creswell, Eisenberger, & Lieberman, 2010), fewer posttraumatic stress symptoms (Garland & Roberts-Lewis, 2013),
better sleep quality and physical health (Murphy, Mermelstein, Edwards, & Gidycz, 2012), and report higher psychological well-being (Brown & Ryan, 2003).

A growing body of neuroscientific research on dispositional mindfulness also suggests that this quality of attention promotes emotion regulation, a key underpinning of the mental and physical health outcomes just noted. The PFC is involved in the metacognitive ability to identify and/or label ongoing subjective experiences (Cole & Schneider, 2007; Ochsner et al., 2004; Wager, Davidson, Hughes, Lindquist, & Ochsner, 2008). Top-down regulation of the amygdala, a brain region crucially involved in fear processing (LeDoux, 2013), anxiety, and affect (Bishop, 2007, 2009; Urry et al., 2006) by the PFC, has been implicated as a classical neural signature of cognitive reappraisal processes (i.e., reinterpreting the meaning of a sensory event) that are considered an important, adaptive form of emotion regulation (Banks, Eddy, Angstadt, Nathan, & Phan, 2007; Drabant, McRae, Manuck, Hariri, & Gross, 2009; Goldin, McRae, Ramel, & Gross, 2008). In a seminal study, Creswell, Way, Eisenberger, and Lieberman (2007) revealed that greater dispositional mindfulness was associated with greater top-down regulation of the right amygdala by the ventrolateral PFC (vlPFC) during an emotion regulation task (i.e., affect labeling). Moreover, some studies indicate that mindful individuals exhibit a unique form of cognitive reappraisal (Garland, Gaylord, & Park, 2009; Garland et al., 2010; Shapiro, Carlson, Astin, & Freedman, 2006; Vago & Silbersweig, 2012; Zeidan, Martucci, Kraft, McHaffie, & Coghill, 2014), namely, the cognitive ability to disengage from higher-order interpretations of sensory events while maintaining an objective cognitive stance. After instructing participants to reappraise negative emotion-inducing pictures (International Affective Picture System [IAPS; Lang, Bradley, & Cuthbert, 1997]), Modinos, Ormel, and Aleman (2010) found that participants higher in dispositional mindfulness were more successful at regulating affective responses to negative mood-inducing pictures. Modinos and colleagues, similar to Creswell and colleagues (2007), found that mindful subjects reappraising negative stimuli showed higher PFC activation (i.e., dorsomedial PFC [dmPFC]), which in turn was associated with less activity in the amygdala. Higher dispositional mindfulness appears to reflect top-down regulation of brain regions involved in early stages of emotional processing (Brown, Goodman, & Inzlicht, 2013), mechanisms also seen in later stages of mindfulness development (through meditation training; see Figure 10.1). Interestingly, we have found that self-reported mindfulness can be significantly increased (up to 16%) after only 3 or 4 days of mindfulness meditation training (Zeidan, Gordon, Merchant, & Goolkasian, 2010; Zeidan, Johnson, Diamond, David, & Goolkasian, 2010; Zeidan et al., 2011), suggesting that mindfulness-induced top-down regulation of affective processes can be enhanced even after brief mental training, an important consideration for the clinical utility of mindfulness.

**Neural Correlates of Brief Training in Mindfulness Meditation**

In this chapter, I propose (Figure 10.1) that brief training in mindfulness meditation engages brain mechanisms that support unique cognitive reappraisal processes that are involved in higher-order cognitive and affective control, enhanced interoceptive
and sensory evaluation, acceptance-based emotion regulation, and reductions in low-level afferent processes (Taylor et al., 2011, 2013; Zeidan et al., 2011, 2014). Brief mindfulness training (1 week or less of training) has also led to improvements across a wide spectrum of cognitive (Mirams, Poliakoff, Brown, & Lloyd, 2013; Tang et al., 2007, 2009; Zeidan, Johnson, Diamond, et al., 2010), pain, and stress reduction outcomes (Tang, Tang, & Posner, 2013; Zeidan, Johnson, Gordon, & Goolkasian, 2010; Zeidan et al., 2011, 2014). Using perfusion fMRI, we recently assessed the brain mechanisms supporting mindfulness meditation, the neural correlates of meditation-related pain attenuation, and anxiety relief after a brief mental training intervention (4 days, 20 minutes per day) that involved breath awareness and other Vipassanā-based meditation techniques (Zeidan et al., 2011). Across 4 days, healthy, pain-free subjects were taught to focus on the changing sensations of the breath and to “acknowledge” sensory events nonjudgmentally. Regarding the brain mechanisms supporting mindfulness meditation, our findings revealed that this training engaged multiple brain regions that process executive level cognitive control (PFC, ACC) and sensory evaluation (anterior insula; secondary somatosensory cortices). Meditation activated the bilateral orbitofrontal cortex (OFC), a brain region involved in reframing the interpretation of our sensory experiences (O’Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001; Peters & Buchel, 2010; Rolls & Grabenhorst, 2008; Schoenbaum, Takahashi, Liu, & McDannald, 2011). We also detected widespread activation of the ACC, specifically the rostral ACC (rACC) and perigenual ACC (pgACC), during meditation, replicating previous findings with other novice meditators (Manna et al., 2010). Regarding pain attenuation, greater meditation-related activation in aspects of the ACC was directly associated with reducing pain and state anxiety ratings (Zeidan et al., 2011, 2014). Regarding anxiety relief, regression analyses revealed that brain activation corresponding to meditation-related pain relief was different than that associated with meditation-induced anxiety reductions (Zeidan et al., 2014). Importantly, meditators uniquely activated brain regions associated with attending to ongoing sensory events. For instance, significant activation in the right anterior insula, a brain region associated with processing sensory experiences relating to the self (Critchley, 2004; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004), and the primary somatosensory cortex (S1), corresponding to the somatotopographic representation of the nose and mouth (where subjects were taught to direct their attention), were significantly activated during meditation. Meditation also activated lower-level sensory processing regions such as the bilateral secondary somatosensory cortices (S2; Coghill, Gilron, & Iadarola, 2001). In summary, this research suggests that even brief and basic training in mindfulness meditation is associated with processing sensory information (S2, anterior insula) and the engagement of brain mechanisms (OFC, ACC) involved in the cognitive reappraisal of sensory information (O’Doherty et al., 2001; Rolls & Grabenhorst, 2008).

Considerable insight into the mechanisms involved in the neurobiology of mindfulness meditation can be gained by examining how meditation modulates nociceptive (painful, noxious) processing. Pain is constructed and modulated by a constellation of interactions among sensory, cognitive, and affective dimensions of our moment-to-moment subjective experience, the same factors that are modulated by mindfulness
meditation. My colleagues and I found that mindfulness meditation, after 4 days of mental training, significantly attenuated S1 activation, corresponding to painful stimulation (right calf) (Zeidan et al., 2011). Furthermore, regression analyses revealed that meditation-related pain relief was associated with significant reductions in low-level nociceptive processing, evidenced by widespread thalamic deactivation. Within the same set of analyses, meditation-related pain relief was associated with increases in executive level brain regions, including the OFC and ACC. These findings illustrate that mindfulness meditation modulates ascending sensory information at thalamic levels before accessing cortical regions implicated in interpreting the meaning of afferent information (Crick, 1984).

Other studies assessing the effects of brief meditation training on neural processes in response to emotion-provoking experimental tasks reveal similar mechanisms corresponding to top-down regulation of lower-level afferent processing. For example, using BOLD fMRI, Taylor and colleagues (2011) examined behavioral and neural responses to emotion-inducing IAPS pictures (Lang et al., 1997) in a group of naive meditators after 7 days of self-facilitated mindfulness meditation training (i.e., listening to an audio recording of guided mindfulness meditation). When compared to attending to “neutral” pictures, “mindfully attending” to positive and negative emotion-inducing pictures produced significant activation in brain regions involved in cognitive control of emotion (e.g., medial PFC [mPFC], lateral PFC, rACC), interoceptive awareness (anterior insula), working memory (hippocampus), as well as deactivation of the amygdala. This network of brain activity was associated with reports of reduced emotional intensity when attending to negative and positive affect-inducing stimuli. Taken together, these findings reveal that brief training in meditation activates the ACC and the PFC to regulate lower-level, emotionally salient sensory processing. These findings also indicate that mechanistic distinctions between self-reported dispositional mindfulness and mindfulness meditation exist. For instance, while PFC activation during mindfulness meditation is similar to brain activity associated with dispositional mindfulness, activation in the ACC and sensory processing areas (anterior insula, somatosensory cortices) signify that the cognitive state of meditation engages brain regions associated with unique, effortless, and purposeful attention toward sensory and cognitive processes. However it bears noting that there are still comparatively few neuroscientific studies of both dispositional mindfulness and brief mindfulness training. As we will see, the neurobiological changes induced by mindfulness meditation after brief training are quite consistent with neural changes seen in mindfulness practitioners trained in the 8-week MBSR course.

### Neural Correlates of Mindfulness Meditation after 8-Week MBSR Training

The MBSR program is an 8-week, intensive meditation course (Kabat-Zinn, 1990) that involves weekly guided group meditation sessions, daily guided meditation exercises practiced at home with the aid of audio recordings (e.g., focusing on the breath
and body sensations as the meditative object), and a daylong meditation retreat conducted largely in silence. MBSR has been shown to improve a variety of mental and physical health outcomes (Grossman, Niemann, Schmidt, & Walach, 2004). Similar to brief meditation training, MBSR has been shown to activate brain regions implicated in executive-level processes (Figure 10.1). For example, evidence for neural processes involved in MBSR-related improvements has been found in clinical anxiety (patients with generalized anxiety disorder), with training-related reductions in amygdala activity (Goldin & Gross, 2010; Goldin, Manber-Ball, Werner, Heimberg, & Gross, 2009) and activation in brain regions supporting reappraisal (i.e., aspects of the PFC and rACC) (Goldin, Ziv, Jazaieri, & Gross, 2012; Goldin & Gross, 2010; Goldin et al., 2009; P. Goldin, Ziv, Jazaieri, Hahn, & Gross, 2013).

Studies assessing the efficacy and neural correlates of MBSR participation in healthy adults paint a similar picture. When instructed to mindfully attend to the sounds of the MRI scanner, Kilpatrick and colleagues (2011) revealed that meditation induced robust functional-neural connections between the bilateral anterior/posterior insula, the mPFC, and ACC. Attending to one’s internal bodily sensations after MBSR produced significant activation in right-lateralized vlPFC, ventromedial PFC (vmPFC), anterior insula, and S2, brain areas previously associated with practicing mindfulness meditation (Farb et al., 2007). Comparing the effects of breath awareness in a group that completed an MBSR program with a wait-listed control group, Farb, Segal, and Anderson (2013) found through functional connectivity analyses a robust decoupling between the insula and mPFC. Whereas the right anterior insula processes interoceptive awareness (Critchley, 2004; Critchley et al., 2003, 2004), the mPFC is a central neural hub for integrating self-narrative thought processes. These findings suggest that participation in an 8-week MBSR course can produce conscious processing changes reflecting a shift from a self-focused mental stance to a more receptive, less evaluative engagement of ongoing sensory events (Farb et al., 2013), neural markers associated with adept meditators, which I discuss next.

**Neural Correlates of Long-Term Mindfulness Meditation Training**

The neuroscientific investigation of adept meditators (more than 1,000 hours of practice; Taylor et al., 2011) suggests that long-term mindfulness meditation training significantly changes the manner in which sensory and perceptual processing occurs in the brain. Whereas brief meditation training appears to produce activation in executive-level brain regions (e.g., PFC) and reductions in lower-level sensory processing, evidenced by deactivations in the thalamus and primary somatosensory cortices, here I propose (Figure 10.1) that long-term meditators exhibit neural activity associated with higher-order awareness reflecting a greater acceptance of sensory experiences without the contextual elaboration or interpretation of those respective events. Indeed, some initial studies suggest that this proposed shift in cognitive processing is positively correlated with cumulative time spent in meditation practice (Brefczynski-Lewis, Lutz, Schaefer, Levinson, & Davidson, 2007; Brown & Jones, 2010; Froeliger et al., 2012; Grant et al., 2010; Grant & Rainville, 2009; Hasenkamp & Barsalou,
The Neurobiology of Mindfulness Meditation

2012; Lazar et al., 2000; Lutz, Greischar, Rawlings, Ricard, & Davidson, 2004; Saggar et al., 2013). The proposed shift in cognition between brief and extensive training can be first demonstrated during formal meditation practice. While beginning stages of mindfulness practice tend to reflect a more effortful, self-directed attentional and emotion-regulatory stance, long-term meditators are postulated to meditate with more efficiency and less effort (Brewer et al., 2011; Gard et al., 2011; Grant, Courtemanche, & Rainville, 2011; Lutz et al., 2008; Manna et al., 2010; Zeidan, Grant, Brown, McHaffie, & Coghill, 2012). Additionally, the neural changes corresponding to adept meditators are more stabilized, such that the cognitive state of mindfulness meditation has been transformed into a trait or temperament that continues outside of formal mindfulness meditation practice (Davidson et al., 2003; Dunne, 2011; Grant et al., 2011; Lutz, McFarlin, Perlman, Salomons, & Davidson, 2013).

During mindfulness meditation practice, long-term meditators exhibit increased activation in brain regions associated with (1) cognitive control, indexed by the rACC (Baerentsen et al., 2010; Brewer et al., 2011; Hölzel et al., 2007; Manna et al., 2010; Short et al., 2010) and aspects of the PFC (superior frontal gyrus, middle frontal gyrus, dlPFC; Baerentsen et al., 2010; Brefczynski-Lewis et al., 2007; Manna et al., 2010); (2) brain regions involved in reward processing (putamen; Baerentsen et al., 2010; Brefczynski-Lewis et al., 2007); and (3) sensory processing (anterior insula; Brewer et al., 2011; Hasenkamp & Barsalou, 2012; Manna et al., 2010). Findings from EEG studies reveal that long-term meditation practitioners process sensory information more quickly after stimulus presentation (Cahn & Polich, 2009), with reduced interference from distracting stimuli (Cahn, Delorme, & Polich, 2013; Cahn & Polich, 2009; Lutz, Slagter, et al., 2009; Slagter et al., 2007), reflecting an overall improvement in perceptual and attentional stability (Lutz et al., 2004; Maclean et al., 2010). These findings provide further evidence that extensive meditation practice can alter cognitive processing, indicated by brain activity corresponding to higher-level executive cognitive control, enhanced lower-level sensory processing, and reduced influences of distracting sensations.

One of the underlying principles of mindfulness-based mental training is the attenuation of affective interpretations (Gunaratana, 2002; Nhất Hanh, 1987; Shapiro et al., 2006). Neuroimaging research focused on elucidating the neural correlates of meditation-related pain relief revealed that long-term meditation practitioners exhibit a less evaluative cognitive stance, demonstrated by reductions in the dlPFC, in the presence of intrusive, painful stimulation (Gard et al., 2011; Grant et al., 2011; Lutz et al., 2013), while brain regions involved in lower-level sensory processing (S2, thalamus; posterior insula) were significantly activated. Interestingly, this decoupling between brain regions supporting appraisal-oriented and sensory processing was directly related to lower pain reports (Gard et al., 2011; Grant et al., 2011). Reductions in the interpretation of the subjective pain experience are associated with reduced anticipation of impending sensory stimuli (Brown & Jones, 2010; Gard et al., 2011; Lutz, Greischar, Perlman, & Davidson, 2009; Zeidan et al., 2012). While the neural correlates of meditation are quite similar between brief meditation training and long-term training, the transformative neural changes associated with long-term meditation practice have been most clearly exhibited when practitioners
are instructed to attend to intrusive sensory events in a nonmeditative state or at rest. This is where we see a greater disengagement between higher-order and lower-level appraisal brain mechanisms, reflecting a temperamental change in higher-level sensory awareness that resembles the cognitive state of meditation but which, taking trait form, appears more stable and enduring.

**Mindfulness and the Default Mode Network**

The default mode network of the brain is characterized by a robust pattern of oscillating neural activity among the mPFC, posterior cingulate cortex (PCC)/precuneus, and medial parietal cortices, and is activated (and functionally connected) during passive resting states, such as passively viewing a fixation cross (Buckner, 2012; Fransson & Marrelec, 2008; Raichle et al., 2001; Scheeringa et al., 2008). The way in which meditation practitioners experience passive resting states (default mode, network-related cognitive processing) differs from that of nonmeditators, and suggests an enhanced capacity to engage moment-to-moment awareness in a nonjudgmental manner. The neural findings to date suggest that that meditators actively engage ongoing sensory events, with an accompanying significant reduction in mind wandering and self-referential evaluations that have been associated with negative mood states (Killingsworth & Gilbert, 2010; Smallwood, Fitzgerald, Miles, & Phillips, 2009). Some of the most common patterns of neural activity across meditative training levels are reflected within the default mode network (Figure 10.1). Reductions in default mode network activation during meditation are reported in studies examining all three forms of training discussed here: brief meditation training (Taylor et al., 2013; Zeidan et al., 2011), 8 weeks of MBSR training (Farb et al., 2007, 2010), and long-term meditation practice (Brewer et al., 2011; Garrison et al., 2013; Grant et al., 2011; Pagnoni, 2012). While we found that greater meditation-related reductions in neural activation in aspects (PCC) of the default mode network were associated with lower anxiety reports after brief mental training (Zeidan et al., 2013), others have found that long-term meditators report significant reductions of mind wandering, with corresponding reductions in default-mode network brain activity, even during rest and when compared to novice meditators (Taylor et al., 2013). These findings support the notion that while all levels of mindfulness significantly reduce default mode related brain activity, only extensive mindfulness practice over years produces durable changes in moment-to-moment processing and corresponding neural activity.

**Structural Correlates of Mindfulness: A Longitudinal Perspective**

Mindful individuals and mindfulness meditation practitioners have recently been found to exhibit unique differences in brain structures when compared to controls, or to individuals reporting lower levels of mindfulness. In one of the largest known mindfulness and neuroimaging studies (155 participants), Taren, Creswell, and Gianaros (2013) revealed that higher trait mindfulness levels were associated with smaller gray-matter volumes in right-lateralized amygdala and left-sided caudate,
The Neurobiology of Mindfulness Meditation

brain regions associated with processing a wide spectrum of emotions. The structural density and gray-matter concentrations of the amygdala and other brain regions in dispositionally mindful individuals parallel the effects observed in meditation practitioners. Moreover, highly stressed individuals assessed before and after an 8-week MBSR course showed significant reductions in reported perceived stress, and these were associated with reductions in the right amygdala gray-matter density (B. K. Holzel et al., 2010). Increases in gray-matter concentrations in the left hippocampus, PCC, temporoparietal junction, and cerebellum have also been exhibited after MBSR participation (Hölzel et al., 2008). These findings may mark the beginning stages of more stable neural and behavioral improvements exhibited by adept meditators. In fact, studies assessing structural changes in long-term meditators have found significant increases in cortical thickness in sensory processing regions such as the dorsal ACC, bilateral S2 (Grant et al., 2010), S1, and right anterior insula (reflecting greater self-awareness) (Lazar et al., 2005), when compared to controls (Hölzel et al., 2010, 2011).

Building Models of the Mindful Brain: Opportunities and Challenges

There are still significant gaps in our understanding of the neurobiology of mindfulness. For one, we have yet to determine the neurofunctional connections mediating the relationship between mindfulness meditation and improvements in mental health. There are aberrant functional connections corresponding to brain regions associated with self-referential processing and disorders such as depression (Anand et al., 2005; Sheline, Price, Yan, & Mintun, 2010; Zeng et al., 2012), chronic pain (Loggia et al., 2013), and addiction (Konova, Moeller, Tomasi, Volkow, & Goldstein, 2013; Sutherland, McHugh, Pariyadath, & Stein, 2012). Since mindfulness meditation has been found to improve several mental health outcomes significantly (Brewer, Elwafi, & Davis, 2013; Farb et al., 2010; Kabat-Zinn, Lipworth, & Burney, 1985; Westbrook et al., 2013), it would be fruitful to determine whether such meditation-related improvements are directly associated with changes in neurofunctional connectivity. We also have not determined the active neurotransmitters corresponding to mindfulness meditation-related improvements in mental health. Bridging these explanatory gaps may advance the field to understand how meditation improves health. Additionally, we still do not know how mindfulness meditation practice leads to more stabilized temperamental neural effects exhibited by long-term practitioners. In other words, how much training is needed before we see long-lasting changes in the brain? Must training be ongoing for such changes to endure?

Another important issue in neuroscientific investigations of meditation deals with the significant reduction in respiration rate during meditation and how this may affect neuroimaging measures of neural activity. In short, meditation alters respiration patterns (specifically, carbon dioxide output) (Farb et al., 2013; Grant & Rainville, 2009; Zeidan et al., 2011), which in turn are likely to affect CBF effects in the brain; might these changes bias our neuroimaging measures of brain activity? While employing perfusion fMRI may not correct the effects of respiration changes on CBF during meditation, it can identify whether CBF changes are exhibited. Another
possibility for evaluating this issue is to measure markers of respiration rate and amplitude (via a respiration belt), which can then be included as covariates or outcomes in mindfulness meditation imaging study analyses.

New imaging technologies offer new opportunities to build models of the mindful brain, which can help in the development of mindfulness-based treatments that specifically target a spectrum of health outcomes. Imaging methodologies such as real-time fMRI have already begun to contribute novel mechanistic insights into how mindfulness affects self-referential processing, social interactions, and attention (Garrison et al., 2013). Real-time fMRI allows us to record moment-to-moment neural information in conjunction with first-person accounts. This technique can provide ample opportunities for individuals to learn, via real-time neurofeedback, how to modulate health-related outcomes such as pain (deCharms et al., 2005), affective disorders (Johnston et al., 2011), and craving (Brewer et al., 2013) through mindfulness-based treatment approaches. Studies assessing changes in gene expression through epigenetic methodologies are also making an impact in delineating the benefits of meditation-based cognitive practices (Black et al., 2013; Creswell et al., 2012; Qu, Olafsrud, Meza-Zepeda, & Saatcioglu, 2013). While MRI scanner technology is improving rapidly, and the use of imaging techniques are becoming more common, assessing and integrating neural, endocrine, physiological, and behavioral data will continue to provide novel and clinically relevant insights into mindfulness-based improvements in health outcomes such as cancer, chronic pain, posttraumatic stress disorder, and substance dependency outcomes.

This chapter has offered an initial account of the neurobiology of mindfulness meditation, and the coming years offer many opportunities to extend our understanding in this area. We will no doubt be better able to gauge how mindfulness meditation practice affects the neurobiological mechanisms that mediate mental and physical health outcomes. Furthermore, identifying the neural substrates of mindfulness-based interventions will help tailor interventions to specific mental and physical health outcomes and thereby perhaps reduce health care costs and medication dependency (Blumenthal et al., 2002; Herman, Craig, & Caspi, 2005; Teasdale et al., 2000). Understanding the nature and structure of the mindful brain is thus a worthy pursuit that may also help to bring more clarity to the still enigmatic world of human consciousness.

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REFERENCES


The Neurobiology of Mindfulness Meditation


