Meditation and the Brain

Neurophsyiological Effects of Meditation

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Meditation is aimed at altering mental states and traits. To achieve this, practitioners engage in different attentional and emotional regulatory practices. Based on the assumption that different mental states are accompanied by different neurophysiological states, meditation practices are believed to induce both short-term and long-term neurophysiological changes. In addition, by frequently engaging in mental training it is believed that meditation practitioners can provide useful information about mental states and conscious subjective experiences. As a result, meditation has been the subject of neuroscientific studies investigating the possible changes in attention, emotion, and consciousness. The present thesis provides an overview on the recent literature on these topics and a structured analysis of the research findings. This overview shows that different forms of meditation yield different effects related to differences in attention distribution, emotion regulation, and cultivated awareness. Furthermore, intensity of the meditation state and the level of experience have consistently been shown to correlate with changes in brain activity. Lastly, structural changes have repeatedly been observed as a consequence of long-term meditation practice. These findings show that the alterations of mental states in meditation practices are accompanied by neurophysiological changes. The overview also demonstrates that the ways through which meditation exert these effects are now beginning to be understood and that results are becoming more cohesive and directed.

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Introduction

Outline of thesis

The current thesis aims at theoretically investigating the neurophysiological effects of meditation. An overview of the recent and relevant literature will be given in an attempt to create a structured analysis of their findings. To this end, a literature search with the term 'meditation' was undertaken using Pubmed and references of the retrieved articles. The search included only articles published in English up to February 2011.

The first part of this thesis will give a description of meditation, its history, and the types of meditation that have been under investigation most. The second part will explain the interest in meditation from a neuroscientific viewpoint and will elaborate on the methodologies used to investigate meditation. The third part will give the overview of the literature on the neurophysiological changes mediated by meditation, separated in a part that covers the effects on attention, a part that covers the changes in emotion, and a part that considers the changes in consciousness. The last part of this thesis will create an overview of the consistent outcomes by summarizing the findings. A link will be made between the current findings and the clinical application of meditation. Furthermore, some concerns related to the research methodologies will be raised. The thesis will be completed with a short conclusion and directions for future studies.

Meditation

What is meditation

The term 'meditation' refers to an extremely wide variety of practices. The central goal of these meditation practices is to voluntarily alter mental states and traits. However, the manner in which this goal is pursued in the variety of practices differs enough from each other so that as of today no clear definition of necessary and sufficient criteria for meditation exists that has achieved universal or widespread acceptance [1,2]. For instance, the focusing of attention on the breath, the recitation of a mantra, the visualization of 'energy' or a divine being and the cultivation of a compassionate state can all be counted as meditation.

Nonetheless, meditation can be conceptualized as a family of complex emotional and attentional regulatory practices affecting mental events by engaging a specific attentional set and has been developed and practiced for various reasons, including the cultivation of well-being and emotional balance and for religious purposes [3,4,5,6].

Although some meditation traditions claim to have no goal or specific purpose, the family of practices share some common features, with a first commonality that each practice resembles a skill or technique that needs to learned and trained. Second, each practice is assumed to induce a reproducible and distinctive state, clearly indicated by certain physical or cognitive features and phenomenally reportable by the practitioner. Third, the induced state is believed to have a predictable effect on the mind and body so that, when induced repeatedly, it can be used by the practitioner to enhance desirable and reduce undesirable mental and behavioral traits. Finally, inducing the intended state is meant to improve with practice [2].

Meditation practitioners often perform daily meditation for a period of time ranging from 15 minutes to several hours. Meditation is a largely internal, personal practice and is commonly exercised without any external involvement. Most practices are performed while sitting, in a manner where the spine is kept straight and the rest of the body neither too relaxed nor too tense. Practices can also be performed while one is moving, for instance in the case of walking meditation, working meditation or yoga. In most meditative traditions, daily practice can be supplemented by retreats that involve intensive practice and offer guidance from experienced teachers. Such retreats can last from a few days to several months or even years and are often held in complete silence [2,4].

History of meditation

Meditation has been extensively practiced in many civilizations for thousands of years. It is, however, difficult to trace the history of meditation without considering the religious context within which it was practiced and because the term meditation refers to so many different practices (see above). It is thus not clear when meditation first arose, yet research suggests that primitive hunting and gathering societies already used repetitive, rhythmic chants to appease the gods, thereby inducing different states of consciousness that may be considered as meditative states [7].

Most of the neuroscientific research on meditation reviewed in this thesis involves Buddhist contemplative traditions or practices that are derived from early Buddhist traditions. Furthermore, Buddhist history and philosophy are important features that are intertwined in the context of most Buddhist meditation traditions. Therefore, a short overview of the history of Buddhist meditation is in place.

Siddhartha Gautama, born around 500 BCE in ancient India (Nepal), was the founder of Buddhism. Different meditative techniques were already being practiced at that time and through meditation Siddhartha achieved enlightenment around the age of 35. From then on Siddhartha was known as the Buddha and he would spend the rest of his life sharing his experiences of enlightenment in teachings known as ‘dharma’ . He also founded the monastic way of life, with meditation as a central component. The central goal of Buddhist meditation is the elimination of suffering by exercising control of one’s own mind and senses [8]. To achieve this, the Buddha taught two types of meditation, samatha meditation and vipassana meditation. Samatha literally translates to "quiescence" and its practice refers to inducing a state in which the practitioner maintains focus on an object for a theoretically unlimited amount of time. Vipassana translates to "insight" and vipassana meditation involves a type of meta-awareness that enables the practitioner to gain insight into one's assumptions about identity and emotions resulting in a realization of "selflessness" [2]. These two types of meditation form the basis for the wide variety of meditative practices that have been developed since and are integrated in most practices where where the cultivation of samatha and vipassana respectively enable the stability and clarity of the meditative state [2].

After the Buddha died, the original unity of Buddhism began to fragment with the most significant split occurring around the 4th century BCE. This split resulted in two forms, one now known as the Mahayana tradition of northern Asia and the other tradition now known as Theravada spreading all over India and southeast Asia. In the 3rd century BCE Buddhism was spread all over India and beyond to other countries as far as Sri Lanka, Egypt and Greece. From Sri Lanka it was spread to Burma, Thailand, Malaysia, Cambodia and Laos where it was named Theravada Buddhism. Around the 1st century CE, Mahayana Buddhism arrived in China, where it flourished around the 6th-8th century CE and evolved into other forms of Buddhism such as Pure Land Buddhism and Ch'an or Zen Buddhism. These forms of Buddhism were then spread to Japan.

It was only in the middle of the 19th century that Buddhism first came to be known in the west when the European colonial empires brought the cultures of India and China to our attention and Chinese immigrants were coming to the west coast of the United States. Following the turbulences of World War II in the 20th century, Buddhism gained more popularity, with Zen Buddhism becoming particularly popular in the United States. Asian masters and westerners who had studied in Asia were now able to found monasteries and spread the Buddhist lifestyle and practices even more. Today it is estimated that there are around 350 million Buddhist in the world, with estimates between 2 and 10 million followers in the west.

Different types of meditation

The common feature across the many divergent meditative practices is the regulation of attention. Depending on how the attentional processes are directed, meditative practices have been classified into two categories: concentrative (also referred to as focused attention (FA)) meditation and mindfulness (also referred to as open monitoring (OM)) meditation [5,6]. These two styles of meditation roughly refer to samatha and vipassana and are often combined, either within a single practice session or over the course of a practitioner's training, and are found in many contemplative traditions including Zen, Vipassana and Tibetan Buddhism.

FA meditation entails focusing and sustaining selective attention on a specific mental or sensory activity such as a repeated sound, an imagined image or a bodily sensation caused for instance by respiration. Sustaining selective attention involves the constant monitoring of the quality of this attention. When distractions arise and attention wanders away from the chosen activity, a practitioner is generally instructed to recognize this mind wandering and to subsequently disengage the attention from the distraction and redirect attention to the intended activity. When progressing in this form of meditation, attention rests more readily and stable on the chosen activity and thus the ability to sustain focus becomes more and more 'effortless'. In advanced practitioners, FA meditation is reported to create a sense of physical lightness and energy and the need for sleep is said to be reduced [5].

OM meditation entails non-reactive and non-judgmental monitoring of the content of ongoing experiences, without focusing on any explicit object or activity. OM meditation is characterized by an open presence and the cultivation of a 'reflexive' awareness associated with a more vivid conscious access to the rich features of each experience, such as ongoing emotional or cognitive processes. Even though there is no contrasting foreground, this awareness remains in the background. A central aim of OM meditation is to gain more insight into the usually implicit features of one's mental life and it is said to enable the practitioner to more readily transform emotional and cognitive habits. In advanced practitioners, OM meditation allegedly leads to enhanced sensitivity to bodily and environmental features while it reduces reactivity of the form that creates mental distress [5].

Zen Meditation

Zen meditation knows two major forms, Rinzai Zen and Soto Zen. Both forms of practice usually start with focusing the attention on the breath as a means to develop the basic level of concentration required for more advanced forms of meditation. In Rinzai Zen, practitioners are instructed to concentrate on koans. Koans are riddles that cannot be solved with knowledge or thinking. Koans are ways to help the practitioners get rid of the thought processes common to ordinary consciousness and to instead access pure awareness of the present moment. Soto Zen is a practice based on mindfulness and open awareness. Practitioners are instructed to observe their thoughts and emotions without clinging to them but to let them go and to bring their attention back to the present moment [4].

Vipassana Meditation

In Insight or Vipassana meditation, practitioners also begin by observing their breath and the sensations it evokes around the nostril area to help develop a focused and sustained attention. Practitioners are then instructed to mentally scan each and every part of their body carefully and feel the sensations in each of those parts. The aim of this practice is to keep the attention moving and to objectively observe the experienced sensations, thereby avoiding the development of feelings of aversion or desire for specific sensations [4].

Mantra Meditation

Mantra or prayer meditation is one of the most widespread and popular forms of meditation and is present in Tibetan Buddhism, as well as in Sufism, Hinduism and many other traditions. Practitioners are instructed to recite a mantra, either aloud or sub vocally, thereby focusing their full attention on the recitation or on the meaning of the mantra. A mantra can be a religious or mystical sound, a word, a sentence, or a poem. The particular bodily sensations that are induced by the recitation of a mantra are believed to calm and focus the mind and body [4].

Transcendental meditation

Transcendental meditation is aimed at quieting and ultimately transcending the ordinary stream of internal mental dialogue by means of reciting a mantra. However, unlike mantra meditation, mantras used in transcendental practice have no meaning but are used for their sound, which is such that attention easily and automatically attends to it. Transcendental meditation thus places a primary emphasis on the absence of concentrative effort and instead aims at developing a witnessing, thought-free, unbounded awareness in which the mantra becomes more secondary and ultimately disappears. The sensations induced by the sound of the mantra are believed to calm the mind and body without the need for intense concentrative efforts and are believed to result in profound relaxation, marked by breath quiescence, and reduced conceptual content [4,9].

Compassion meditation

Loving-kindness or compassion meditation aims at the generation of non-referential feelings of loving-kindness or compassion towards all living beings and is also a common practice in Tibetan Buddhism. This kind of meditation begins with the visualization of a respected, a beloved and a neutral person in order to evoke feelings of compassion to each of these persons separately. Practitioners are then instructed to gradually broaden their focus from this one particular person towards a combination of these persons and finally towards all living beings and everyday life, thereby developing a non-referential, reflexive state of compassion. The cultivation of compassion is believed to create a general sense of well-being and to aid in prevention of feelings of anger or irritation [2,4].

Clinical applications based on meditation

Mindfulness-based stress reduction (MBSR) is a therapeutic intervention based on mindfulness meditation, developed by Jon Kabat-Zinn [10]. MBSR is a group program with a duration of eight to ten weeks, with weekly group sessions of 2.5 hours, one all-day session, and daily homework assignments. The program is aimed at a progressive acquisition of mindfulness, characterized by equanimity, non-evaluative and sustained moment-to-moment awareness of perceptible mental states and processes, and is claimed to benefit health and well-being. To achieve this, specific exercises are incorporated in the program, including different forms of mindfulness meditation, yoga exercises, and cultivation of mindfulness in stressful and social situations. This intervention program has been employed among patients with a variety of chronic disorders, as well as among healthy individuals who seek to develop their ability to cope with normal stressful life events. Studies have employed participants of MBSR as useful subjects to examine the effects of a short period of meditation training and it is for this reason that MBSR is mentioned here.

The neuroscientific study of meditation

History of scientific research

Meditation has been the subject of scientific research since the 1950s, although widespread scientific interest was only reached in the 1990s (see Figure 1). Today, over 2000 scientific publications on the term 'meditation' have been published, mainly in the scientific fields such of psychology and neuroscience.

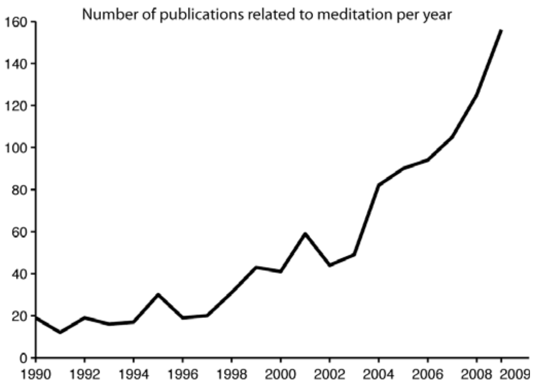

Figure 1 Search results for the term 'meditation' from Pubmed, 1990-2009 (adopted from Braboszcz et al., 2009 [4])

This scientific interest in meditation research reflects a recent shift in cognitive science towards viewing first-person experience and consciousness as a valuable topic in scientific investigations. Although the importance of subjectivity and introspection in the scientific study of mental phenomena had already been emphasized at the end of the 19^{th} century by William James (1842-1910), it has been largely ignored in the following decades [11]. Due to the emergence of behaviorism in the first part of the 20^{th} century, research tried to understand cognition and mental phenomena by examining their observable consequences in the world. Behaviorism advocates the study of the mind in investigating only behavioral performances and electrophysiological responses, resulting in a complete rejection of subjective and private experiences from the field of science. The subsequent development of cybernetics and cognitive science led scientists to view the brain as an information-processing unit and this reductionist approach to cognition has continued to influence cognitive science up until two decades ago. Reconsideration of first-person experiences in cognitive science was set in motion by Damasio [12] and Varela, Thompson and Rosch [13], posing an embodied approach to the mind which views first-person experiences as a critical component for the complete understanding of mind and brain. From this perspective, Varela [14] introduced the concept of neurophenomenology into neuroscience in 1994, combining first-person reports of subjective experience with the experimental study of brain activity. This development paved the way for the now established and respected study of cognitive and mental phenomena, including the study of meditation. A more detailed description of the neurophenomenological approach and its relation to meditation research can be found below.

Fundamental versus clinical research

The neuroscientific research on meditation involves both fundamental and clinical research and concentrates on a better understanding of how mental training can affect the brain, mind, body and overall health. The aim of fundamental research is to increase our knowledge and theoretical understanding of fundamental principles and is initially not concerned with the practical implications of its findings. Changes in brain activation, functioning and anatomy induced by mental training and phenomenal experiences are a major focus of the fundamental research on meditation. Clinical research, on the other hand, utilizes the findings from fundamental research to study treatment and therapeutic protocols that might prove to be beneficial in clinical practices. Investigating the effects of clinical applications of meditation such as Mindfulness-Based Stress Reduction (MBSR) [15,16] and Mindfulness-Based Cognitive Therapy (MBCT) [17] are examples of clinical research on meditation.

The main focus of the current thesis will be on fundamental research, reviewing the literature on the neural correlates and physiological effects of meditation. Clinical applications that have arisen from fundamental findings will only be briefly addressed in the discussion section.

Research methods

The fundamental research on meditation has employed a variety of neuroimaging methods to investigate the effects of meditation on the brain. Electroencephalographic measures of brain activity have been the most widely used method to study meditation since the 1950s.

Electroencephalography (EEG) is the recording of summed post-synaptic electrical activity along the scalp produced by large groups of neurons. EEG has a temporal resolution in the range of milliseconds that allows for examination of the fine dynamics of neural processes. An EEG signal can be divided into bands by frequency (i.e. Delta: <4 Hz, Theta: 4-7 Hz, Alpha: 8-12 Hz, Beta: 12-30 Hz, and Gamma: >30 Hz)and synchronization or desynchronization within these bands can be used to characterize mental states. Synchronization refers to the mechanism by which a population of oscillating neurons fires their action potentials in temporal synchrony. Synchronization can occur on short-range and long-range. Short-range synchronization occurs over a local small network whereas long-range synchronization concerns neural assemblies that are farther apart and resides on distant connections. Long-range synchronizations, also referred to as coherence, are proposed as a mechanism for the formation of global assemblies that may underlie the emergence of conscious integrated experience [2]. Sensory evoked potentials (EPs) or event-related potentials (ERPs), derivatives from the EEG signal, are fluctuations in the EEG signal time-locked to the presentation of a stimulus and provide information about the processing of stimuli [18].

Over time, other methods have been developed that are now also used to study meditation, such as positron emission tomography (PET), single photon emission computed tomography (SPECT), magnetic resonance imaging (MRI), and functional magnetic resonance imaging (fMRI). PET measures emissions from radioactively labeled chemicals that are injected into the blood stream and uses this data to produce two- or three-dimensional images of the distribution of chemicals throughout the brain and body. PET usually takes around 30 seconds to produce an image and can reveal information about blood flow, oxygen and glucose metabolism, and neurotransmitter concentrations by using different tracers. SPECT is similar to PET, though it is less sophisticated and produces images with lower spatial resolution than PET.

MRI uses magnetic fields and radio waves to produce two- or three-dimensional images of both surface and deep brain structures. MRI has a high spatial resolution in the range of millimeters. fMRI relies on the magnetic properties of oxygenated and deoxygenated blood to measure blood flow and oxygen consumption in the brain as it changes over time. fMRI is based on the assumption that active brain regions use oxygen and a change in blood oxygenation in a certain region can therefore be interpreted as activation or deactivation. An fMRI scan can produce an image of brain activity every two seconds, which allows for observing brain activations as participants perform certain tasks or are exposed to certain stimuli.

Next to their technological differences, these different neuroimaging techniques all have their own advantages and disadvantages with respect to meditation research. Meditation is a practice that is usually performed for at least 15 consecutive minutes while sitting in an upright position in a silent room or environment that is specifically set up to have the least amount of distractions. fMRI research is performed in a blocked design, where blocks of meditation are alternated with blocks of control or rest conditions. These blocks are usually no longer than just a few minutes and utilizing fMRI thus entails short meditation periods. Meditators often report that the depth and intensity of their meditation evolves over time and the employment of fMRI might therefore limit the investigation of the meditative state. This problem does not occur with EEG, PET, SPECT. Another disadvantage of (f)MRI concerns the scanner noise. Generating the magnetic forces needed for MR imaging produces a loud clicking or grinding sound, which might easily disturb the meditative state. Again, EEG, SPECT, and PET are noiseless techniques. Furthermore, EEG, SPECT, and PET are methods that allow the meditators to sit in an upright position, while individuals need to be in a supine position to enter a MRI scanner (SPECT and PET sometime also require a supine position, depending on the scanner). A final advantage of EEG is the possibility to make use of a portable system that can be operated in any environment. This allows for recording of activity outside the environment of laboratories and permits investigation in the known context of the meditator.

Together with measures of behavioral performance and/or subjective reports of experiences, these neuroimaging methods and the combination of the results from their employment have facilitated the elaborate study of meditation.

Neurophenomenology and the study of meditation

As described earlier, cognitive science has recently recognized the need to make use of introspective reports in order to understand the neural correlates of mental phenomena. Neurophenomenology refers to such an approach, where detailed first-person descriptions of experience are combined with quantitative measures of brain activity. At a methodological level, this approach aims to obtain richer first-person data through rigorous phenomenological explorations of experience and to use this first-person data to reveal new third-person data about the physiological processes crucial for these experiences [14,19].

Although first-person reports are thus of central importance to the neurophenomenological approach, it seems reasonable to assume that people vary in their abilities to observe and report their experience resulting in the possibility that introspective reports can be biased or inaccurate.

However, it is also believed that these abilities can be enhanced through mental training of attention, emotion and metacognition. It is for this reason that meditation is of special interest to neurophenomenology, since Buddhist meditative practices are concerned with precisely this sort of cognitive and emotional training: cultivation of a sustained, attentive awareness of the content of ongoing experiences [11,19]. Therefore, practitioners of meditation are believed to be able to produce more precise information about their subjective experience and through the generation and sustainment of particular meditative states they are believed to be able to provide important information about subjective aspects of consciousness that are not readily accessible through ordinary introspection or reflection. It is also believed that proficiency in this sort of mental training should be reflected in changes to brain structure, function and activation. Hence, neurophenomenology has adopted meditative practices as an important research tool for developing better phenomenologies of subjective experience and for investigating the neural correlates of these experiences.

Neurophenomenology builds on the philosophical tradition of phenomenology that emphasizes the systematic study of consciousness and the content of conscious experiences. The main focus of neurophenomenology is therefore on the study of consciousness.

Neurophysiological effects of meditation

<u>State versus trait effects</u>

One aim of meditation is to induce an altered distinct and reproducible state during practice. Another aim of meditation is that regular practice will have a long-lasting positive effect on the mind and body. Based on the assumption that different mental states are accompanied by different neurophysiological states, meditation may induce two kinds of neurophysiological changes. State changes are relatively short-term changes that occur during or immediately following meditation practice and refer to altered sensory, cognitive, and self-awareness experiences. State changes may include experiences of perceptual clarity, conscious awareness, a deep sense of calm or peacefulness, or attentional focus towards the object of meditation. Trait changes develop with practice and are changes are present even when the practitioner is not actively engaged in meditation practice. Trait changes can be the more frequent or permanent experience of meditation states outside formal practice periods. In addition, trait changes also refer to changes that are not directly related to the changes that are induced through practice and may be considered as 'side-effects'. Examples of trait changes from long-term meditation practice include a deepened sense of calm or peacefulness, eradication of negative states, a heightened awareness of sensory perceptions, an increased sense of comfort, or a shift in the experience of thoughts, feelings and self-awareness [6].

<u>Attention</u>

In the same way that physical training strengthens the muscles, mental training may strengthen certain circuits in the brain. Since meditation involves a form of attentional training, the cognitive function that may be affected the most by meditation practice is attention. The neurophysiological effects of meditation on attentional processes and correlates are therefore studied the most.

According to Lutz and colleagues [5], attentional training involves at least three attentional regulatory skills which have been associated with dissociable systems in the brain. First, orienting or focusing attention comprises the selection of specific information from the abundance of sensory input and is associated with activity in cortical structures such as the temporal-parietal junction (TPJ), the ventro-lateral prefrontal cortex (PFC), the frontal eye fields, and the intraparietal sulcus (IPS) [20]. Second, sustaining attention comprises the maintenance of a state of high sensitivity over time and is associated with sustained synchronous activity between the thalamus and the right frontal and right parietal areas, also known as the thalamo-cortical loop [21,22]. Third, disengaging and redirecting attention away from a source of distraction involves executive attention supporting the monitoring and resolution of conflicts among thoughts, feelings and mental plan. This process is associated with activity in de dorsal anterior cingulate cortex (ACC) and the dorso-lateral PFC [23,24]. Differences in activation patterns or anatomy in these regions may thus be expected in the brains of practitioners, either during or as a result of meditation.

Meditation traditions that involve FA meditation clearly employ all of these processes in their practices. OM meditation practices also employ most of these processes, though in their case attention is distributed. Based on the difference in attentional focus in meditative practices, neurophysiological changes are expected to differ among meditative styles.

An early study by Valentine & Sweet [25] examined the possible diverse effects of concentrative (FA) and mindfulness (OM) meditation on sustained attention by presenting a series of tones at a regular rate, followed by a set of tones that were unexpected due to the difference in presentation rate. Both groups of meditators showed better performance in detecting the tones in comparison with controls, with long-term meditators performing superior than short-term meditators. In addition, mindfulness meditators demonstrated superior performance over concentrative meditators when the stimuli were unexpected. The authors suggested that the practice of distributed attention in mindfulness meditation enables these practitioners to not get caught up by a certain pattern but to instead maintain a state of high receptivity. A different study by Carter and colleagues [26] investigated the performance of practitioners of both concentrative and compassion meditation on binocular rivalry and motion induced blindness. Again, differential results were found for the different meditative practices. No observable changes were found following compassion meditation while concentrative meditation led to an extreme increase of perceptual stability of the competing images in the binocular rivalry test and increased disappearance duration of the motion induced blindness. The authors concluded that some, though not all, types of meditation can measurably alter the normal fluctuations in attention induced by these perceptual rivalries.

A study by Lazar and colleagues [27] was one of the first to employ fMRI to investigate the brain activations during simultaneous concentrative (awareness on the breath) and mantra meditation in practitioners of Kundalini Yoga. Among other regions, increases in activation were observed in neural structures that are known components of distributed attentional networks, such as the dorso-lateral PFC and parietal cortex. When the duration of meditation increased, brain activations were found to increase accordingly. This is in agreement with the self-reported increase of the intensity of meditation over time of a practice session.

In a study by Lutz and colleagues [28], EEG patterns of experienced practitioners and beginners to compassion meditation were compared. The experienced practitioners displayed robust gamma-band oscillations and long-distance phase-synchrony during meditation that differed from those of beginners, in particular over lateral fronto-parietal areas. In addition, the ratio of gamma-band (15-42 Hz) activity to slow oscillatory activity (4-13 Hz) was initially higher for the practitioners than the controls in the resting baseline before meditation over medial frontoparietal regions. This difference was found to gradually increase during meditation and remained higher in the post-meditative state. Gamma-band synchronizations are thought to reflect attentional and affective processes. The gradual increase of gamma activity during meditation is in agreement with the increasing intensity of the meditation over time and reflects the view that neural synchronization requires time to develop. The increase in gamma activity was also suggested to reflect an increase in the thalamo-cortical interaction, again indicating increased sustained attention over time. Next to the state-changes observed during meditation, this study reported a difference in baseline activity between meditators and controls, thereby demonstrating trait effects of meditation in brain electrical activity.

These altered baseline EEG patterns in long-term meditation practitioners suggest long-lasting changes in brain activity. Based on this assumption, Lazar and colleagues [29] hypothesized that meditation practice might also be associated with changes in brain structure. Using MRI, they assessed cortical thickness in practitioners with extensive experience in Insight meditation and matched controls. Greater cortical thickness for meditators compared to controls was found in regions including the right middle and superior frontal sulci, inferior occipito-temporal visual cortex, and right anterior insula. Differences in the prefrontal cortex were most pronounced between older participants, suggesting that meditation may slow down age-related cortical thinning and the possibly related cognitive decline in executive attention. Furthermore, cortical thickness in the visual cortex and insula correlated with years of practice, supporting the notion that the observed differences resulted from meditation practice. Most of the regions identified in this study were found in the right hemisphere, which is proposed to be essential for sustaining attention [22].

Pagnoni & Cekic [30] extended these findings by demonstrating that Zen meditation may have neuroprotective effects as it showed to reduce the age-related decline of cerebral gray matter volume, in particular in the putamen. These results were complemented by superior performance for Zen meditators compared to controls in a rapid visual information processing task assessing sustained attention. Beyond its classical role in motor control and learning, the putamen is also implicated in cognitive flexibility and attentional processing and may thus be related to processes such as the conscious regulation of attention and posture in Zen meditation.

Returning to the state changes associated with meditation expertise, a strong assay of attention, the attentional blink, was used by Slagter and colleagues [31] to investigate the distribution of limited attentional resources and the possible effect of Vipassana meditation. The attentional blink refers to missing the second of two targets, when two targets (T1 and T2) embedded in a rapid stream of distractions are presented in close temporal proximity. This is believed to result from competition between T1 and T2 for limited resources. Slagter and colleagues demonstrated that three months of meditation training resulted in a smaller attentional blink and decreased resource allocation to T1, as shown by a smaller T1-elicited P3b. Importantly, individuals that showed the largest reduction in resource allocation to T1 generally showed the greatest improvement in detecting T2. First, these findings indicate that the ability to accurately identify two temporally close meaningful items depends upon the efficient deployment of resources to the first item. Second, these findings show that improvements in performance on a novel task may be achieved by pure mental training and lend support to the notion that the adult brain is capable of plastic change.

Slagter and colleagues extended the results from this study by further analyzing the spectral EEG data [32]. This examination revealed that successful target detection was associated with enhanced theta phase locking. Successful detection of the second target was also succeeded by enhanced theta phase locking, in particular for those individuals who showed the greatest reduction in T1-elicited P3b amplitude. These results indicate a role for local phase synchrony of theta activity in conscious target perception and suggest that after meditation-based mental training the cognitive system is more rapidly available to process new target information. Baseline oscillatory activity right before task onset was not found to differ among meditators and controls.

ERP measures were also employed by Srinivasan & Baijal [33], who examined the effects of concentrative Sudarshan Kriya Yoga on preattentive processing of change detection represented by the mismatch negativity (MMN) brain potential. Meditators were found to have larger MMN amplitudes than controls both before and after meditation. These results were interpreted as a better ability of meditators to make involuntary shifts of attention and an enhancement of deviance detection processes. Moreover, meditators showed a further increase of MMN amplitudes at frontal areas immediately after meditation. This provides evidence for altered engagement of frontal and temporal areas during meditation practice that result in altered preatttentive processing.

Cahn & Polich [34] obtained ERP measures elicited by a passive auditory oddball paradigm from experienced Vipassana meditators during meditation and a control condition designed to mimic everyday thinking. The auditory oddball task consisted of a frequent standard tone, an infrequent oddball tone and an infrequent distractor, and was used to elicit ERP components (N1, P2, and P3a) indexing perception and attentional engagement processes. During meditation, N1 and P2 amplitude to the distractor were somewhat reduced. P3a amplitude to the distractor was also reduced and, importantly, this reduction was strongest in meditators with the most hours of daily practice and was absent in meditators who reported drowsiness during the experimental meditation practice. Whereas the earlier described P3b is hypothesized to index temporal-parietal activity reflecting resource allocation, P3a indexes frontal neural activity produced by stimulus-driven attention mechanisms. The reduction in P3a amplitude is thus consistent with a decreased involvement of frontal cortex in response to unexpected and distracting stimuli during meditation. In line with the reduced P3a and MMN amplitude, this finding reflects a disengagement of attentional networks to stimulus-driven activation during or as a result of meditation.

A similar study was conducted by Lutz and colleagues [35], who assessed performance on a dichotic listening task during meditation and analyzed the corresponding spectral EEG and ERP measures. Attention had to be focused on one ear to detect target tones among the presentation of frequent and deviant tones to both ears. Three months of Vipassana training showed to reduce behavioral response variability and to increase theta phase locking to target tones over anterior regions compared to controls. Importantly, and in line with the results from Slagter and colleagues [32], those individuals showing the greatest increase in neural response consistency also showed the largest decrease in behavioral response variability. Furthermore, meditators demonstrated a reduction in event-related desynchronization to target tones in beta band activity, suggesting a reduction in the amount of resources or engagement necessary to perform the task.

Baijal and Srinivasan [36] also showed differences in theta band activity during meditation. Experienced concentrative Sudarshan Kriya Yoga meditators exhibited theta coherence in frontal areas and decreased alpha power compared to controls. Increased relative theta power over frontal regions and decreased relative theta power over parietal regions compared to controls were found during the deepest phase of meditation. Frontal-midline theta is thought to be generated by the ACC and this increase in theta power was suggested by the authors to correspond with increased ACC activity. The decrease in theta power in parietal regions was suggested to correspond with inhibition of sensory and attentional processes in these areas. Together, these suggestions are in agreement with the results from a fMRI investigation by Hölzel and colleagues [37] discussed below, as they show increased ACC activity for expert meditators during meditation compared to controls.

All of the aforementioned studies investigated the long-term effects of meditation practice on attentional processes and neural structures by assessing either the trait or state changes in experienced meditators with years of training. In contrast, Tang and colleagues [38] examined the short-term effects of brief meditation training in individuals with no prior meditation experience. To this end, subjects were randomly assigned to a control group or an experimental group for five days of integrated body-mind training (IBMT). The Attention Network Task (ANT) was used to measure the ability to orient, alert, and resolve conflict. No differences were found before training while the experimental group showed an increase in conflict resolution after training. This finding demonstrates that short-term IBMT can influence the efficiency of executive attention.

Zeidan and colleagues [39] followed this approach by also examining the effect of brief mindfulness training on measures of attention. Randomly assigned subjects that underwent mindfulness training showed improvements in performance on tasks indexing visuo-spatial processing, working memory, and executive attention compared to controls, while no differences were found before training. These results further support the suggestion that immediate benefits can be found after only short-term meditation practice.

Van den Hurk and colleagues [40] introduced three different cues and an extra measure of performance to the ANT, enabling them to distinguish between the alerting, orienting, and executive attention network processes and between performance and efficiency. Expert mindfulness meditators showed better orienting of attention and a trend toward better executive attention than controls. The first finding was interpreted as a more flexible orienting network in meditators as result from repeatedly engaging and disengaging attention in their practice. The disengagement of attention from distractions in meditation practice may have also increased the ability of meditators to focus attention on relevant while ignoring irrelevant information as reflected by the increase in executive attention. Furthermore, expert meditators showed to be more efficient compared to controls, reflected by increased accuracy for responses with identical reaction times.

In addition to these behavioral, EEG and structural MRI findings, Brefczynski-Lewis and colleagues [41] employed fMRI to investigate brain activity during concentrative meditation on a fixation cross in expert concentrative meditators and controls. Both groups activated a large overlapping network of attention-related brain regions, including frontal parietal regions such as ACC, lateral occipital regions, and insula. Although meditators showed less activation in these areas than controls, variation was found in both the strength and time course of activation within the group of expert meditators. Meditators with the least hours of practice showed more activation on a faster timescale, whereas meditators with the most hours of practice showed less activation. This difference fits an inverted u-shaped function which has been demonstrated before with skill acquisition in other domains of expertise and was believed by the authors to support the description by expert meditators of a decreased need for voluntary attentional effort to attain concentration. In addition, neural activity in response to distractions resulted in decreased activation in default-mode regions related to task-irrelevant thoughts and affective regions in expert meditators.

Hölzel and colleagues [37] tried to replicate the findings from Brefczynski-Lewis and colleagues, in particular with respect to the inverted u-shaped function of activation found in the ACC. However, during meditation, expert Vipassana meditators exhibited more (instead of less) activation in both the ACC and dorsal-medial PFC compared to controls. In addition, expert meditators also showed greater ACC and dorso-medial PFC activation during meditation than controls during a mental arithmetic control condition. The authors infer that these results suggest that Vipassana meditation training leads to more cortical processing of conflict resulting and better attention regulation during meditation. Consequently, they support the view that greater expertise in attention regulation is accompanied by greater ACC activation, in accordance with the findings from Baijal and Srinivasan [36], rather than supporting the explanation of compensatory ACC activation in novices brought forward by Brefczynski-Lewis and colleagues.

Taken together, these studies show that meditation practice can have a remarkable influence on attention as exemplified by the diversity of the demonstrated behavioral and neurophysiological changes. A summary of these findings and their implications will be given in the discussion section below.

Emotion

In most meditative practices, practitioners are instructed to keep a calm, balanced, non-judgmental state of mind and to notice affects without aversion for unpleasant emotions or desire for pleasant ones. One of the claimed benefits of this feature of meditation practice is reduced emotional reactivity resulting in a greater emotional stability for challenging life events. In some other traditions, such as compassion meditation, practitioners are instructed to generate a state of loving-kindness towards all living beings. This practice is believed to increase positive feelings and well-being, which aids in dealing with negative encounters.

The regulation of emotions may be achieved via two means: attentional and cognitive control [42]. Enhanced attention and better resistance to distraction might reduce emotional reactivity by modulating the amount of attention that is allocated to process emotional stimuli and by reducing negative emotions' propensity to interrupt the ongoing stream of thoughts and behavior. Cognitive control may regulate emotions by changing the expectations and interpretations about emotional stimuli or by learning to associate new emotional responses with emotional stimuli. Neuroimaging studies have shown that these two forms of emotion regulation depend upon interactions between prefrontal and cingulate control systems (e.g. PFC, orbito-frontal cortex (OFC), ACC) and cortical and subcortical emotion systems (e.g. amygdala, insula, nucleus accumbens, thalamus) [42].

Since many meditation traditions involve a form of attentional training, attentional modulation of emotions may be detected in meditation practitioners. Furthermore, the non-reactive and non-judgmental monitoring of the content of ongoing experiences, including emotions, may mediate changes in the regulation of emotion through cognitive control. Differences in activation patterns or neural structure in the regions associated with these forms of emotion regulation may thus be expected.

The early fMRI study by Lazar and colleagues [27], mentioned before, investigated brain activations during simultaneous FA (awareness on the breath) and mantra meditation in practitioners of Kundalini Yoga. Among other regions, increases in activation were identified in neural structures involved in arousal and autonomic control, such as pregenual anterior cingulate, amygdala, midbrain, and hippocampus. These findings provided early evidence of activation in attentional, cognitive, and limbic regions during meditation.

Aftanas & Golocheikine [43] specifically examined differences in emotional experience and spectral EEG between short-term and long-term practitioners of Sahaja Yoga. Long-term practitioners compared to short-term practitioners demonstrated increased positive affect, which was accompanied by increased anterior frontal and midline theta synchronization. Increased long-distance theta connectivity was also found with a more left-sided anterior lateralization. Frontal and midline theta synchronization was proposed to originate from alternating activities of the PFC and ACC, whereas the long-distance connectivity was regarded as strengthened connections between PFC and posterior association cortex that are required for positive emotions. Lateralization towards the left hemisphere support this notion as this anterior left-sided dominance in electrical activity has previously been related to emotionally positive experiences. That is, the baseline electrical activity of the brains of individuals who tend to react positively and let go quickly of negative emotions have been shown to exhibit greater left-sided anterior activation than those of individuals more prone to nourishing negative emotions (as reviewed in [44]).

Davidson and colleagues [45] also reported changes in anterior activation asymmetry. These changes were demonstrated immediately following an eight week MBSR training and four months afterwards. Meditators, compared to controls, showed an increase in left-sided anterior activation over time, which was most pronounced over frontal areas in response to both positive and negative affect induction. The increases in activation were furthermore associated with self-reported decreases in anxiety and negative affect. The authors suggested that this left-sided anterior activation is associated with more adaptive responding to negative events resulting in a more positive outlook on life. The results from these two studies show that meditation experience has beneficial effects on dealing with emotional experiences that are characterized by specific oscillatory patterns of activity.

Another EEG study was performed by Aftanas & Golocheikine [46], this time to examine the differences in spectral EEG between experienced Sahaja Yoga practitioners and controls when negative emotions were induced. Arousal was increased over four different conditions; eyes-closed, eyes-open, neutral emotional stimulus, and a negative emotional stimulus. In the eyes-closed condition, meditators demonstrated larger alpha and theta powers compared to controls. When arousal was increased, alpha and theta power decreased in both groups, though alpha and theta power in the eyes-open condition and alpha power in the neutral stimulus condition remained higher for meditators. This was suggested to correspond to an overall lower state of arousal for meditators. The induction of negative emotions significantly decreased alpha power in both groups and was also shown to increase gamma power over anterior regions in controls. Arousal is regarded as a necessary condition for gamma activity and increased arousal may indicate activation in neural circuits involved in both cognition and emotion. This combined alpha decrease and gamma increase was therefore suggested to reflect heavier emotional workload for controls compared to meditators, supported by an increase of self-reported negative affect in controls.

Lutz and colleagues [28] also found increased gamma synchrony in experienced practitioners of compassion meditation. Experienced practitioners displayed increased gamma power over lateral fronto-parietal areas during meditation and in addition, the ratio of gamma-band activity to slow oscillatory activity was shown to be higher for the practitioners compared to controls before, during, and after meditation. As compassion meditation is aimed at cultivating a state of loving-kindness characterized by a positive emotional tone, these differences in gamma activity further support the idea that gamma activity is involved in emotional experiences.

A great deal of fMRI investigations have also revealed activations in areas related to emotional processing and emotion regulation. Hölzel and colleagues [37] found greater activation during meditation of rostral ACC and dorsal-medial PFC for expert Vipassana meditators compared to controls. Greater rostral ACC and dorsal-medial PFC activation may correspond to the cognitive regulation of well-being and happiness in mediators as the authors bring forward that these regions have been found activated during monitoring of emotions.

Lutz and colleagues [47]examined the activation in response to emotional stimuli during meditation and rest in expert compassion meditators compared to controls. All individuals showed increased activation to the emotional sounds in insula and ACC during meditation. The activity in the insula was found to be associated with the intensity of the meditation practice and was greater for expert meditators than for controls. Insula activation was also associated with the relevance of the emotional sounds, with greater activation to emotional sounds compared to neutral ones. The difference between groups in insula activation is in line with the findings by Lazar and colleagues [29], who showed larger cortical thickness in this region among expert meditators compared to controls. In addition, expert meditators showed stronger activations in components of the network that mediates empathy, including the amygdala, temporal parietal junction, inferior frontal gyrus, posterior superior temporal sulcus, precuneus, and posterior cingulated cortex.

Based on the findings of enhanced activation and cortical thickness in areas that are implicated in emotional processes, Hölzel and colleagues [48] used voxel-based morphometry to reveal significantly greater gray matter concentration for meditators in the right hippocampus compared to controls and a positive correlation between medial OFC and amount of meditation practice. The hippocampus is involved in modulating cortical arousal and responsiveness and also modulates amygdalar activity and its involvement in emotional processes. The OFC, in turn, plays a role in emotion regulation by down-regulating amydala activity. These changes in gray matter concentration might thus reflect the improved ability of meditators to regulate emotional responses.

All aforementioned studies investigated experienced meditation practitioners and the long-term effects on emotion regulation. However, short-term meditation training has also been shown to improve self-regulation of emotion. Hölzel and colleagues [49] extended the previous results by comparing self-reported stress levels and gray matter concentration in the amygdala before and after an eight week MBSR training. MBSR training was shown to decrease self-reported levels of stress, which was correlated with a decrease in gray matter concentration in the right basolateral amygdala. The amygdala is widely viewed as one of the most important limbic structures with regard to stress and anxiety and the basolateral part has been proposed as the site for relay of sensory information from cortical and subcortical areas to the central nuclues of the amydala. This finding was thus suggested to demonstrate that actively altering the emotional response to stress through cognitive control in only eight weeks of MBSR can lead to changes in brain morphometry, which proves to be beneficial for well-being. It should be noted though that while this correlation was found, no significant overall effect of the training on amygdaloid gray matter was shown.

Significant differences in gray matter concentration in this population of subjects have been demonstrated though in other regions, as reported in the follow-up study by Hölzel and colleagues [50]. Increases in gray matter concentration were found in the hippocampus, posterior cingulate cortex, TPJ, and cerebellum. Although no changes were found in the insula or amygdala, the hippocampal changes were thought to reflect the ability of practitioners to modulate emotional control as this structure has been implicated in the regulation of emotion apart from its well known function in learning and memory. The increases in gray matter concentration in TPJ are thought to arise from its involvement in feelings of empathy and are in agreement with the abovementioned findings.

Even shorter meditation training have also been demonstrated to change emotional tone in meditators. A five day IBMT practice has been demonstrated to enhance positive moods, reduce negative ones and improve reactions to mental stress, as a study by Tang and colleagues [38] revealed. Subjects were randomly assigned to an experimental or control condition and before training no differences existed between both groups. After training, an assay of mood state revealed reductions of anger, depression, fatigue, anxiety and an increase in vigor. Furthermore, measures of cortisol and secretory Immunoglobin A showed a reduction in induced stress, in particular when the stress challenge was followed by another period of practice. These results show that improvements in the affective domain can arise from only a short period of meditation practice.

A fMRI study by Creswell and colleagues [51] used a different approach to investigate the effects of mindfulness on emotion regulation. Participants with no meditation experience indicated trait levels of mindfulness and were subsequently scanned during an affect labeling task and control condition. As indicated above, the non-reactive and non-judgmental monitoring of emotional experiences is a common feature in meditation practices, which can be seen as mentally labeling emotions and involves cognitive control associated with activity in the PFC-limbic circuitry. Greater levels of self-reported mindfulness traits were found to be associated with increased widespread activity in the PFC and decreased amygdala activity during affect labeling compared to a control condition of gender labeling. Connectivity analyses revealed that subjects high in mindfulness compared to subjects low in mindfulness showed a strong inverse relationship between activity in these PFC regions and the right amygdala. These results support the notion of cognitively controlling emotional experiences through prefrontal cortical regulation of limbic responses.

The results of these studies show that meditation positively influences the regulation of emotion through both attentional and cognitive control. Meditation practice seems to affect the connection between cortical areas and the emotional limbic system in such a way that it changes the appraisal of and interpretation of emotions. They further suggest that repeated practice of meditation can have long-term effects and suggest that this involves brain plasticity.

<u>Consciousness</u>

A central aim of meditation practice is to voluntarily induce an altered state of mind during practice, which, with repeated practice, may lead to trait changes in mental states that are evident even when a practitioner is not actively engaged in meditation. These changes in mental states are experienced and reportable by the practitioner and reflect a change in conscious subjective perception. Subjective perceptions or experiences are characterized by the notion that there is a 'self' who is experiencing the world, our emotions, our sensations, and paradoxically also our selves. Ordinary consiousness can be described as this subjective experience of one's environment, feelings, actions, thoughts and existence. A self-reported change in the control of attention, in the experience of emotional events, or in any other subjectively experienced altered state of mind may thus be seen as a shift in consciousness.

Most meditative traditions aim at generating a pure awareness of the present moment, without the interruption of a notable 'self' as observer. For instance, in concentrative meditation this pure awareness can be the sustained focus on the breath. In this form of awareness, the 'self' is unperceivable and is only present as subject of the experience and this awareness can be seen as a form of interoception or visceral awareness. However, in achieving this form of pure awareness, awareness may include a 'self' as object, next to a 'self' as subject. This is for instance the case when monitoring one's own attention and discursive thoughts in concentrative meditation. This latter form of awareness does include an observed 'self' and is therefore a form of self-referential awareness.

Visceral awareness and interoception are processes that rely on homeostatic, meta-representations in the brain, mediated in particular by activations in the anterior insula, somatosensory cortex and ACC [52,53]. Within the domain of EEG, gamma band oscillations (>30 Hz) have been related to the conscious momentary experience and long-distance phase synchronies are regarded as a likely candidate for the neurophysiological substrate of the binding of multiple aspects of conscious experience and perceptions into the coherent subjective state of moment-to-moment awareness [19,54].

Neural correlates of self-referential awareness have been identified by two independent lines of research. First, tasks designed to explicitly induce self-referential processing have consistently revealed activation in the medial PFC and posterior cingulate cortex extending to the precuneus. Second, these regions have also been identified as the default-mode network (DMN) in which activation is greater during rest compared to during engagement in goal-directed tasks, indicating self-referential thoughts and feelings in the absence of external stimulus processing [55,56].

When altered states of consciousness induced by meditation are studied, differences in these regions associated with interoception and visceral awareness or self-referential awareness may thus be expected.

One of the first studies investigating the altered states of consciousness induced by meditation was done by Lehmann and colleagues [57]. This case-study examined the distribution of gamma band EEG activity during 4 different forms of meditation, described as clearly different subjective states by the meditator. The results showed differences in the distribution of gamma band activity, reflecting different active neuronal populations during the four meditations. These findings were among the first to confirm that different mental states induced by meditation are accompanied by clearly different, physiological brain states.

Aftanas & Golocheikine [58] also examined altered states of consciousness induced by meditation, only they focused on differences in alpha, delta and theta frequencies between novice and experienced practitioners of Sahaja Yoga. No differences were found for the delta frequencies. Baseline differences were found between these groups with decreased alpha frequencies and increased alpha synchronization for experienced meditators. During the altered state of consciousness induced by meditation, in this case characterized by heightened attention and positive affect, increases in anterior frontal and midline theta synchronization, increased long-distance theta connectivity, and increased overall alpha power was found in experienced meditators compared to novices. Changes in theta power were suggested to relate to the altered emotional state and changes in alpha power to the altered attentional state. Long-distance theta connectivity was suggested to indicate increased intensive information processing in the altered state of consciousness during meditation compared to rest. This study replicated and extended the aforementioned findings that altered states of consciousness are accompanied by differences in electrical activity.

In addition to the findings mentioned in the section concerning emotion, the later study by Aftanas & Golocheikine [46] also reported differences in lateralization in eyes-closed and eyes-open conditions with larger alpha power in the right hemisphere over parieto-temporal cortex cortex for controls. This finding is different than the previously reported left-sided anterior activation related to emotional attitude and was suggested to reflect larger mind-wandering in controls compared to meditators.

Another study performed by Kjaer and colleagues [59], combined spectral EEG and PET to look at the changes in endogenous dopamine release in the ventral striatum during an altered state of consciousness induced by meditation. Experienced practitioners of Yoga Nidra, a form of relaxation meditation were the meditator experiences a reduction in readiness for action and enhanced sensory imagery, demonstrated a correlated increase in theta activity and a 7.9% decrease in binding potential during meditation. This decrease in binding potential corresponds to an increase of approximately 65% of extracellular dopamine release. Two frontal-subcortical circuits include the ventral striatum, one originating in the lateral orbito-frontal cortex and one in the ACC. Dysfunction in the former results in a lack of interest and initiative and dysfunction in the latter in apathy, no display of emotions, and impairments in speech and movement. The increase in dopaminergic tone seemed as such associated with the decrease in desire for action and emotional detachment as reported by the meditators.

Spectral EEG during meditation and control condition in Vipassana practitioners was also investigated by Cahn and colleagues [60]. In addition, this study used advanced signal-processing techniques to rule out the possibility that the observed changes in spectral EEG were related to artifacts from scalp muscle or eye movement activity. Furthermore, measures of drowsiness, experience and condition order were used as covariates to be able to fully attribute the observed changes to differences in states between meditation and control condition. This study revealed an increase in gamma power over parietal and occipital areas, a decrease in delta power and a relative increase in theta power over frontal areas during meditation compared to rest. Decreases in frontal delta were associated with reduced drowsiness, whereas decreases in alpha power tended to be correlated with increased drowsiness. Decreases in alpha power also tended to correlate with enhanced meditative experience and enhanced alpha power was demonstrated in the second condition (regardless of being meditation or control condition). This pattern of gamma and theta activity may indicate the involvement of more sensitive and perceptual clear awareness of moment-to-moment experience. The decrease in delta activity has been suggested to index inhibited activity in prefrontal areas responsible for analyzing, judging and expectations.

Farb and colleagues [61] investigated the effect of an eight week MBSR training on the altered states of consciousness that arise from the two distinct modes of awareness by means of fMRI. In the narrative focus, subjects were instructed to reflect on what a particular trait adjective meant about them as a person, resembling thoughts that occur during mind wandering. In the experiential focus, which resembled mindfulness meditation, subjects were instructed to monitor their moment-to-moment experiences to these adjectives. Meditators and controls both showed activation in the medial PFC and in a left lateralized linguistic-semantic network during the narrative focus. In the experiential focus, controls showed a slight reduction in medial PFC activation and an increase in activations in left prefrontal-parietal regions. Subjects that had been trained in MBSR showed more pronounced reductions in medial PFC and an increase in activations in the lateral PFC and viscero-somatic regions including the insula, secondary somatosensory cortex, and inferior parietal lobule. These results suggest a fundamental neural dissociation in modes of consciousness that support distinct aspects of self-reference. Functional connectivity of the insula revealed a strong coupling with the ventro-medial PFC for controls, whereas for the trained meditators this connection was uncoupled and instead increased coupling was found between the insula and the dorso-lateral PFC. These findings further suggest that the distinct modes of awareness are mediated by different networks that can be modulated by mental training.

A ten week longitudinal random assignment also assessed the differences between the two awareness modes by examining changes in EEG power, coherence, and source localization during transcendental meditation (TM) and rest. Travis and colleagues [9] specifically aimed to examine the activation of the default-mode network in these different conscious states. TM was shown to increase alpha power over frontal areas and to reduce beta and gamma power over frontal and parietal regions. TM was also shown to increase alpha coherence over frontal and parietal regions and to increase frontal beta coherence. Source localization revealed generators of alpha power in anterior, dorsal, and posterior cingulated cortices, precuneus, left insula, and left lingual gyrus and parahippocampus. These regions overlap with regions identified in the default-mode network. Since activation in these areas was higher during TM compared to rest, the investigators suggest that the transcendental contentless experience must be different from autobiographical or mind-wandering thoughts associated with the default-mode network. Furthermore, the increases in coherence are considered important for integrating distributed processing in the brain and are, as described above, possibly mediating the moment-to-moment transcendental awareness.

All studies mentioned above were specifically aimed to investigate meditation-induced altered states of consciousness. However, studies aimed at attention processes or emotion regulation did also reveal results related to altered states of consciousness.

For instance, the earlier mentioned MRI study by Lazar and colleagues [29] investigating cortical thickness differences between expert practitioners of insight meditation and controls found the largest differences in thickness in the right anterior insula. Gray matter volume of the right anterior insula has previously been demonstrated to predict interoceptive performance and subjective ratings of global awareness [53]. The difference in cortical thickness in the anterior insula is thus consistent with the increased awareness of internal states, such as the breath, reported by many meditators.

An investigation on differences in gray matter concentration with voxel-based morphometry between Vipassana meditators and controls by Hölzel and colleagues [48] likewise revealed significantly greater gray matter concentration for meditators in right anterior insula and in the right hippocampus. Differences in gray matter concentration in the right anterior insula are in accordance with its involvement in interoception and visceral awareness. A trend towards significance was found for the left inferior temporal gyrus (ITG). Furthermore, the amount of meditation practice was found to be significantly correlated with the gray matter concentration of the left ITG and correlated at trend level with the right insula. Expected differences in the dorso-lateral PFC, ACC, and left postcentral gyrus were not confirmed. However, whole brain analyses revealed that gray matter concentration in the medial orbito-frontal cortex (OFC) and amount of meditation practice were positively correlated.

Brefczynski-Lewis and colleagues [41] investigated brain activation with fMRI in response to distraction sounds. Among other areas, increases were found in bilateral dorsal intra-parietal sulcus extending into post-central sulcus and anterior insula. Activity in these regions was suggested by the authors to respectively be related to monitoring the quality of meditation and awareness of one's internal state. Also employing fMRI, Creswell and colleagues [51] found that self-reported mindfulness trait levels in individuals with no prior meditation experience showed a strong positive association with medial PFC activation during an affect labeling task. The medial PFC has been found to be activated during self-relevant tasks such as monitoring one's own emotional state and was thus implicated in altered conscious states.

Finally, Hölzel and colleagues [50] found increases in gray matter density in the hippocampus, posterior cingulate cortex, temporal parietal junction, and cerebellum following eight weeks of MBSR training compared to controls. The study mentions that the TPJ has been suggested to play a crucial role in the conscious experience of self and that the posterior cingulate cortex is engaged when the relevance of stimuli to oneself is assessed. Together, the hippocampus, TPJ and posterior cingulate cortex (together with parts of the medial PFC) form a network that supports diverse forms of self-projection and the increases in gray matter concentration in these areas might thus match the shift in internal representation of the self, which is reported by a majority of meditators.

Summarizing, these findings show that the altered mental states induced by meditation can yield valuable information on the processes and neural circuits underlying consciousness. Differences between certain modes of awareness can furthermore be associated with activity in different networks and meditation has been shown to induce plastic changes in brain structure as a result of repeatedly induced alterations in consciousness.

Discussion

Consistent outcomes

The multitude of neuroscientific studies investigating the effects of meditation that are reviewed in this thesis were focused on changes in brain activity and structure with respect to attention, emotion, and consciousness. A wide variety of results have been found, due to the differences in the studied meditative practice, the research methodology, the experimental design, etc. Nonetheless, some consistent outcomes and conclusions can be inferred from the presented findings.

One of the main conclusions is that differences in meditation practice have resulted in different effects. With respect to the domain of attention, examining a concentrative versus open monitoring meditation style has yielded notably different results. The focused and selective attention that is cultivated in concentrative meditation has been shown to produce improvements in ignoring and disengaging from unexpected stimuli and distractions [25,26,36]. In contrast, practitioners of meditative styles that can be regarded as open monitoring cultivate a more distributed attention that has been shown to improve their ability to sustain a state of non-centered attention and to increase their flexibility to shift attention towards unexpected stimuli [25,33,34,35,40]. With respect to emotion regulation, investigations of practitioners of meditative styles that incorporate compassion meditation have revealed increases in processing of emotional stimuli [46,47] and positive mood [28,43,46] whereas practitioners of concentrative styles show reduced emotional reactivity related to enhanced disengagement from distracting negative stimuli [36]. In the domain of consciousness, differences have also been found between certain aspects of meditation practice. Monitoring one’s own attentional focus or emotional content has been seen to activate regions related to self-awareness [41,51] as opposed to generating a state of open and pure awareness of ongoing experiences [9,59,60,61].

Another finding that has been shown consistently is that brain activity may be correlated with the depth of the meditative state, which strengthens over the duration of a meditation session [27,28,47,51]. Related to this finding is the repeatedly shown difference in brain activity or anatomy associated with the amount of hours of practice or level of experience of meditators [34,48,51]. Although these findings do not always converge with each other, they do show that differences based on level of expertise are a common finding and thus lend support for the notion that meditation is a technique that is learned and perfected over years of practice just as for instance learning how to play a musical instrument. They also set the ground for one more consistent finding, namely the differences found in baseline activations [28,33,46] or structural differences [29,30,48,49,50] between meditators and controls that have also been found in other areas of skill acquisition. These differences reflect trait changes resulting from meditation practice, next to the state changes that occur during the actual practice of meditation.

Consistent outcomes have also been found on a more detailed level within the different domains of attention, emotion and consciousness. Different attentional skills have been associated with activations in TPJ, ventro-lateral PFC, frontal eye fields, IPS, dorsal ACC, and dorso-lateral PFC and synchronous activity between the thalamus and right frontal and right parietal regions. Increased theta synchronization over frontal and central areas has been found in different studies [32,35,36,43,58] that has been suggested to originate from the PFC and ACC and supported by observed activations in these areas [37]. Structural changes in PFC have also been demonstrated in meditation practitioners, with a reduction in the age-related cortical thinning and gray matter volume decrease that is associated with age-related cognitive decline [29,30] These regions have been implicated in mediating selective and executive attention and are important structures for focusing and monitoring of attention and resolving possible conflicts in the attentional domain [19,22,23]. Long-distance phase synchrony has been observed in gamma band frequencies [28], which was suggested to reflect thalamo-cortical interactions necessary for sustaining attention [20,21]. Sustaining attention has also been associated with the finding of increases in cortical thickness in the right hemisphere [22,29]. Furthermore, ERP measures indicating allocation of attentional resources have been found to differ, where the greatest reduction in resource allocation was accompanied by the greatest improvement in behavioral response [31,32,35]. Together, these results strongly support the idea that the mental training involved in meditation can have beneficial effects on attentional processes.

Findings with respect to changes in emotional processing of meditators have also shown to converge in certain respects. As meditation may regulate emotions through the training of attention and the process of cognitively monitoring one’s own emotions, changes in areas such as the PFC, OFC, ACC, amygdala, insula, thalamus, nucleus accumbens may be observed. fMRI studies have confirmed these expected activation differences in attentional, cognitive and limbic areas [27,37,43,47]. More specifically, activation in the insula was found to increase in response to emotional stimuli and was furthermore associated with the intensity of the meditative state [47]. Frontal and central theta power associated with activity in the PFC and ACC was also shown to increase with increasing positive emotions [43]. In addition, an inverse correlation between the PFC and amygdala was found during affect labeling [51], supporting the idea that cognitive control can regulate emotions. Structural changes were also demonstrated in these regions and were in one case even shown to correlate with self-reported measures of affect [48,49,50]. One of these studies reported changes in the hippocampus and related this to the role of the hippocampus in modulating cortical arousal and amygdalar activity [48]. Another finding that was reported more often was the left-sided anterior lateralization of meditators compared to controls in spectral EEG [43,45,58]. This finding was linked with established results from EEG analyses in affective neuroscience, showing that individuals that exhibit a more left-sided baseline activation over frontal areas have a more positive outlook on life than individuals with more right-sided activation [44]. All in all, these results demonstrate that meditation can yield changes in emotional processing, either through exerting attentional or cognitive control.

Neuroscientific research into consciousness is still in its infancy (for the reasons mentioned earlier) and studies concerning this topic are only just starting to arise. However, differences in attentional and emotional tone can also be regarded as altered states of consciousness and, as shown with the present findings, are observed to affect areas that are implicated in conscious states [29,41,48,50,51]. Conscious states and alterations in consciousness have been associated in particular with changes in gamma band activity and long-distance phase synchrony [19,54]. Several studies have shown differences in these measures accompanied by differences in subjective mental states confirming this idea [9,57,58,60]. Alterations in consciousness specifically related to awareness of bodily sensations and feelings have been related to differences in activation and morphometry of the insula, somatosensory cortex, and ACC [52,53]. Meditation has shown to alter mental states related to this kind of awareness and changes in activations of these regions, in particular the insula, have accordingly been found [9,59,60,61]. Cortical thickness and gray matter concentration in the insula was also shown to differ between meditators and controls, reflecting trait changes in visceral awareness as a result of meditation [29,48] Subjective experiences related to the 'self ' such as monitoring one's own actions and feelings are regarded as a form of self-referential awareness and have shown to activate areas that have previously been identified as components of the default-mode network with regions such as the medial PFC and the posterior cingulate cortex extending into the precuneus [55,56]. Studies that explored changes in self-referential awareness during meditation have confirmed differences in activity in these areas [41,50,51,61]. Overall, these findings show that reflexive awareness and visceral awareness that are cultivated in meditation practices can yield valuable information into the neural circuits underlying consciousness.

Research limitations and concerns

Although consistent findings have been found among the reviewed studies in this thesis, caution in interpreting these finding should be emphasized. The research on meditation faces a number of difficulties that complicate the reliability of some of the outcomes.

A first thing to highlight is the problem of the heterogeneity of the studied meditative traditions. Meditation refers to such a wide variety of practices, all aimed at slightly or completely different goals defined by their own specific set of instructions and values that makes it impossible to treat them as the same or generating similar effects. This concern had been recognized by many of the investigators and the need for a validated scientific framework in which the different meditation techniques can be properly classified has been repeatedly brought forward. When such a framework would exist, results can be more easily generalized and differences in outcomes can be better understood.

Another difficulty in examining the effects of meditation is the use of subjects that have participated in therapeutic mindfulness interventions such as MBSR, mindfulness-based cognitive therapy (MBCT) or IBMT. Although these interventions are extremely suitable for research purposes, in the sense that they allow for the investigation of effects of short-term meditation practice in individuals that have no prior experience in meditation, they also raise some concerns. As these trainings are group programs, with activities that do not exclusively consist of meditation practice, it is not desirable to attribute the observed changes resulting from these interventions to meditation practice alone. The other activities practiced in these interventions and the context of such a training may act as confounding factors and should be treated accordingly. For instance, studies of group dynamics indicate that being part of a group can act to facilitate certain outcomes.

This last point touches upon other limitations in meditation research, such as the use of proper control conditions, the context in which meditation is practiced and the degree of experience of practitioners. When comparing meditators with non-meditators, it is difficult to make use of a control condition that only differs in the meditative state. When groups of subjects in therapeutic interventions are compared to controls, these controls are usually on a waiting list and are not active and do not profit from the context in a way similar to the experimental condition. This difficulty concerning the control condition is not only present in longitudinal studies, but also in cross-sectional studies were within group analyses try to determine differences between meditation and control conditions. The most commonly used control condition is a state of relaxation. However, experienced meditators have often reported that when they are not engaged in a particular task and are told to relax, they find it hard to refrain from entering a meditative state. This impedes the unequivocal comparison across conditions. Comparison across participants is further hindered by the influence on the behavior of experienced meditators by the context in which meditation is often practiced. Expert meditators, especially those recruited from monasteries, do not only engage in meditation practice and its corresponding context but are usually also surrounded by a lifestyle that differs from non-meditators in ethics, traditions, diet, culture, environment, and so on. Buddhist philosophy or religion, in which most meditative traditions are intertwined, adheres to several restrictions, rules and rituals that can significantly influence the abilities and characteristics of meditators. These differences are also likely to act as confounding variables and may contribute to some of the changes that have been found when dedicated expert meditation practitioners are studied. Lastly, it has shown to be very difficult to control the degree of expertise of practitioners. Meditators with extended experience may have been practicing meditation daily for years and have attended multiple retreats during these years. However a great deal of variation still exists between the amount of expertise in expert meditators and opposing results have been found for long-term versus short-term meditators (e.g. [37,41]). Classifying meditators as short-term practitioners when they have less than two years of practice and as long-term practitioners when experience reaches over two years, may again be problematic and confound results.

Finally, the experimental design of the reviewed studies may limit the conclusions that can be drawn from the observed changes. The results obtained with the cross-sectional design of most of the studies are confounded by a self-selection bias or pre-existing baseline differences as subjects are not randomly assigned to the experimental or control group and only a few studies take the effort to control for baseline values. Furthermore, this type of design only allows for correlational findings as it is impossible to infer causality. For instance, differences in cortical thickness between meditators and controls could be just a marker for people more prone to practicing meditation. In addition, studies that have compared activation difference during meditation and a control condition may be confounded since trait changes have been found among practitioners.

Taken together, these limitations and concerns indicate the difficulties that are encountered when studying the effects of meditation and emphasize the need to consider current evidence with caution. Nonetheless, the results brought forward by the few studies that used randomization or employed a longitudinal design can shed light on otherwise possible confounded results.

Psychological and clinical application of meditation research

The beneficial effects of meditation on general well-being are one of the reasons that civilizations in many parts of the world have long been practicing meditation. Interest in these effects was reflected by the emergence of fundamental research on meditation during the 1950s and the development of clinical applications around the 1980s. MBSR and MBCT are among the most widely used applications of mindfulness meditation and are offered to patients suffering from a wide range of symptoms. These programs were designed to be free of the cultural, religious and ideological factors associated with the Buddhist origins of mindfulness and instead were aimed to offer an environment in which the challenges of mindfulness meditation are translated into a vocabulary and method for exploring both mind and body that is relevant to the participants [16,17]. Mindfulness-based interventions have been increasingly incorporated over the past three decades and nowadays a wide variety of positive effects have been reported (for an extensive overview, the reader is referred to [62]). Among these are improvements that are tought to be related to the neurophysiological changes reviewed in this thesis, such as beneficial changes in well-being and quality of life and reductions of symptoms in a number of disorders such as anxiety, depression, substance abuse, eating disorders, and chronic pain. Therefore, it is worth noting some of these psychological and clinical benefits and their relation to fundamental research.

MBSR and MBCT are mostly used to treat psychological and psychiatric disorders such as depression, bipolar disorder, anxiety and stress. Both these interventions have been shown to significantly reduce the possibility of relapse in patients suffering from depression compared to standard interventions [62,63]. Major depressions have been associated with decreased density or volume in the hippocampus and the increased activations and increases in gray matter concentration reported earlier may thus be related to these positive effects [27,48,50]. Stress reductions have also been reported as a result of MBSR [62,63] which may be related to the differences found in amygdala activity and structure [27,49,51] and hormone levels [38].

Mindfulness-based therapies have also been reported to be efficient in the treatment of individuals with attention deficit (hyperactivity) disorders (AD(H)D) [64]. This seems plausible as meditation trains attention and differences in the activation of attentional regions between meditators and controls have been shown to overlap with regions showing abnormal structural or functional variations in AD(H)D patients [41]. Furthermore, Zen meditation, which can be seen as mirroring in reverse the characteristics of AD(H)D, was shown to increase gray matter volume in the putamen, a structure associated with cognitive flexibility and attentional processing and strongly linked to AD(H)D [30].

These are just a few examples of the reported effects of mindfulness-based therapies and their relation to the findings presented in this thesis. Nonetheless, they indicate the importance of fundamental research on meditation as they start to shed light on the underlying mechanisms responsible for the positive results of clinical applications of mindfulness-based interventions.

Conclusions and future directions

The present thesis has attempted to summarize the recent developments in the neuroscientific study on meditation. Although a formal definition of meditation is still absent, the central features of meditation have been described together with its origin and history and the main styles of meditation that are subject to scientific research. The interest in meditation from a neuroscientific perspective has been elucidated and the neurphysiological effects that have been reported over the last ten years have subsequently been reviewed. This has shown that meditation can have diverse effect on both cognitive and affective processes and in areas concerning different aspects of consciousness. The reviewed studies show that these effects are now beginning to be understood and are becoming more cohesive and directed, even though a scientific framework for fundamental research is still lacking.

Future studies should be directed at creating such an empirical and theoretical framework in order to ease the generalization of research findings. Further methodological improvements tackling the mentioned limitations, such as better control conditions, randomized longitudinal studies with individuals that have no prior meditation experience, or the use of single-blind designs with the experimenter blind to the treatment allocation will all help to create more reliable results and to increase our understanding of the changes in processes and brain structures involved in meditation. For instance, a longitudinal design with individuals that have no prior meditation experience could randomly assign participants to an experimental group that will be part of a meditation retreat, or a control group that will be educated in the traditions, rituals, ethics, and general lifestyle that are associated with the meditation practiced in the experimental group. With such an experimental design, participants in the control group do not actively engage in meditation while they are part of a retreat that is contextually similar to the experimental group. A different suggestion would be to compare individuals that engage in meditation training with individuals that engage in another form of training associated with skill acquisition, such as training in performance on a musical instrument. These different kinds of trainings can be matched in schedule, intensity, form of training (individualized or group), etc. Since skill acquisition in other domains than meditation has been demonstrated to yield effects [65], research of this kind would allow for examination of training effects that are specifically associated with meditation instead of with the effects that are associated with any form of skill acquisition. These suggestions may be promising options for the development of a better suited control condition and also lend themselves for single-blind assessment when the experimenters are only to test the participants at the beginning and end of such training periods.

One of the research areas that can really profit from meditation is the study of consciousness. As the neurophenomenological approach is still in its infancy, this area of research needs special attention and characterization of changes in various brain circuits that are engaged by meditators will aid in the development of knowledge in this domain.

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Appendix

Authors	Year	Method	Meditation style	Experimental design	State or trait effect	Domain	Main findings
Valentine & Sweet [25]	1999	Behavioral	Tibetan Buddhist - concentrative & mindfulness	19 subjects, 22 controls (matched for intelligence); cross-sectional assessment of performance on Wilkins' counting test	State	Attention	Both meditation forms resulted in better overall performance compared to controls. Task performance associated with sustained attention was superior for mindfulness meditators compared to concentrative meditators when the stimulus was unexpected. No difference in performance between groups when stimulus was expected.
Lazar et al [27]	2000	fMRI	Kundalini yoga - mantra & concentrative	5 subjects, no controls; assessment of brain activation during meditation on breath and mantra and control condition	Stait	Attention & Emotion	Increased activity in areas subserving attention (DLPFC and parietal cortex) and arousal and autonomic control (limbic regions, midbrain, pregunual ACC) during meditation compared to control condition.
Lehmann et al [57]	2001	EEG	4 different forms of meditation	1 subject; case-study assessing distribution of EEG activity during 4 different forms of meditation	Trait	Consciousness	Differences in spatial distribution were found in the gamma band frequency during four different meditations, associated with differences in activated neuronal assemblies.
Aftanas & Golocheikine [43]	2001	EEG	Sahaja Yoga	27 subjects, 11 short-term, 16 long-term; assesment of spectral EEG during meditation and self-reported emotional experience	Trait	Emotion	Decreased alpha frequency was found for long-term compared to short-term meditators. Long-term meditators also showed an increase in self-reported positive affect accompanied by an increase in anterior frontal and midline theta synchronization and an increase in long-distance theta connectivity between prefrontal and posterior association cortex. This increase in theta connectivity was further accompanied by more left-sided lateralization.
Kjaer et al [59]	2002	PET & EEG	Yoga Nidra - relaxation	8 subjects, no controls; assessment of endogenous dopamine release and altered states of consciousness during meditation and control condition	State	Consciousness	A 7.9% decrease in 11C-raclopride binding potential was found in the ventral striatum during meditation, corresponding to a 65% increase in dopamine release. Spectral EEG analyses revealed an increase in theta activity that correlated with the decrease in binding potential and a decrease in alpha activity. Self-reported readiness for action was decreased and sonsory imagery increased. possibly reflecting the self-reinforcing nature of meditation practice when proficiency is attained
Carter et al [26]	2003	Behavioral	Tibetan Buddhist - contrentrative & compassion	23 subjects (performing both forms of meditation), no controls (61 subjects tested previously for motion blindness); binocular rivalry and motion induced blindness	State and trait	Attention	Concentrative meditation allowed for an extreme increase in the stable percept of the two competing images, both during and following meditation, and increased the dissapearance duration of the motion induced blindness. In contrast, compassion meditation yielded no effects.
Aftanas & Golocheikine [58]	2003	EEG	Sahaja Yoga - concentrative and compassion	27 subjects, 11 short-term, 16 long-term; assesment of spectral EEG during meditation and rest	Trait	Consciousness	Decreased alpha frequency and increased synchronization were found for long-term compared to short-term meditators in the rest condition. During meditation, long-term meditators demonstrated an increase in anterior frontal and midline theta synchronization, an increase in long-distance theta connectivity between prefrontal and posterior areas, and an overall increase of alpha synchronization. The increase in theta connectivity was further accompanied by more left-sided lateralization.
Davidson et al [45]	2003	EEG	MBSR	25 subjects, 16 controls (both randomly assigned); 6 month longitudinal study assessing EEG symmetries, affect, and immune function	Trait	Emotion	Meditators showed a decrease in negative affect over time compared to controls. Meditators further demonstrated enhanced left-sided central acitvation. Frontal electrical activity was also decreased in meditors after induction of both positive and negative emotions. Increased left-sided activation was associated with reduced anxiety and negative affect.
Lutz et al [28]	2004	EEG	Compassion	8 experienced subjects (10.000h to 40.000h), 10 controls (novices to meditaiton); cross-sectional assessment of EEG patterns during relaxation (eyes open and closed) and meditation	State and trait	Attention & Emotion	Expert meditors showed increases in self-induced gamma power and long-distance phase-synchrony patterns over lateral fronto-parietal areas compared to novices. The ratio of gamma activity to slow oscillatory activity was shown to be higher for expert meditators before, during and after meditation compared to novices.
Lazar et al [29]	2005	MRI	Insight (OM) meditation	20 subjects, 15 controls (matched for gender, age, ethnicity, and education); cross-sectional assessment of cortical thickness	Trait	Attention & Consciousness	Increased cortical thickness in brain regions associated with attention, interoception, and sensory processing (e.g PFC, in particular superior fronal sulci and right anterior insula) was found for expert meditators compared to controls. Thickness in some of these regions was correlated with meditation experience and the largest difference was observed in PFC between older participants.

Authors	Year	Method	Meditation style	Experimental design	State or trait effect	Domain	Main findings
Aftanas & Golocheikine [46]	2005	EEG	Sahaja Yoga	25 subject, 25 controls (matched for gender and age); cross-sectional assessment of sprectral EEG in response to neutral and emotional stimuli	Trait	Emotion & Consciousness	Meditators demonstrated larger alpha and theta power compared to controls in rest conditions. In response to neutral emotional stimuli, decreased alpha and theta power was observed in both groups, though meditators still showed a higher power than controls. Negative emotional stimuli further decreased alpha in both groups, accompanied by an increase in anterior gamma power for controls. Lateralization differences were found with greater right alpha power over parieto-temporal cortex for controls.
Slagter et al [31]	2007	ERP	Vipassana	17 subjects, 23 controls (matched for gender, age, and eduacation); 3 months longitudinal study assessing performance and ERP measures on attentional blink	Trait	Attention	3 month of intensive Vipassana training decreased attentional engagement in the processing of the first of two temporally close targets, thereby improving the detection of the second target. Decrease in brain-potential index of resource allocation to the first target correlated with improvement of detection of the second target.
Srinivasan & Baijal [33]	2007	ERP	Sudarshan Kriya Yoga - concentrative	10 subjects, 10 controls (matched for gender and age); cross-sectional assessment of mismatch negativity (MMN)	State and trait	Attention	Meditators exhibited an overall larger MMN amplitudes than controls, specifically for deviant tones, and showed an extra increase in amplitudes immediately after meditation.
Pagnoni & Cekic [30]	2007	fMRI	Zen	13 subjects, 13 controls (matched for gender, age, and education); cross-sectional study assessing gray matter volume and performance on RVIP	Trait	Attention	Reduction of age-related decline rate of cerebral gray matter volume in putamen for Zen meditation compared to controls, accompanied by a similar pattern in the performance of a rapid visual information processing task assessing sustained attention.
Tang et al [38]	2007	Behavioral	Integrative body-mind training (IBMT)	40 subjects, 40 controls (both randomly assigned); single blind 5 day longitudinal study assessing performance on ANT and emotion	State and trait	Attention & Emotion	IBMT improved performance in executive attention and conflict monitoring on a task where the target is surrounded by distactors. An assay of mood states revealed enhanced positive moods and reduced negative ones for the experimental group. Assessment of cortisol and secretory IgA revealed a reduced stress response to mental challenges, especially after an additional period of meditation practice.
Brefczynski-Lewis et al [41]	2007	fMRI	Tibetan Buddhist - concentrative	14 subjects, 16 controls (matched for age), 11 motivated controls; cross-sectional assessment of brain activation in response to emotional and neutral sounds during meditation and rest	State	Attention & Emotion	Concentrative meditation was associated with greater activation in multiple attention-related brain regions (DLPFC, superior frontal sulcus, intraparietal sulcus). Brain activation varied with practitioner's level of expertise (u-shaped) with less activity in long-term meditators than short-term meditators. Amygdala activity in response to emotional sounds was decreased for meditators compared to controls. This decrease in activation was correlated with increasing amount of meditation practice.
Holzel et al [37]	2007	fMRI	Vipassana	15 subjects, 15 controls (matched for gender, age, education, and handedness); cross-sectional assessment of brain activation during meditation and control condition	State	Attention & Emotion	Increased activity in rostral ACC and dmPFC compared to controls.
Creswell [51]	2007	fMRI	Dispositional mindfulness	27 subjects, no controls; assessment of brain activation during affect labeling and control condition	Trait	Emotion	Dispositional mindfulness was associated with greater widespread prefronal activation during affect labeling and decreased amygdala activation. Connectivity analyses revealed a strong negative association between prefronal areas and amygdala among subject high in mindfulness.
Farb et al [61]	2007	fMRI	MBSR	20 subjects, 15 controls (mathced for gender, age, prior meditation experience); cross-sectional study assessing brain activation during two distinct modes of self-reference	Trait	Consciousness & Attention	Narrative self-focus revealed activity in midline prefrontal areas and in a left-sided linguistic-semantic network. Moment-to-moment experiental focus revealed a reduction in medial PFC and an increase in prefrontal-parietal activations in controls. Meditators showed a more pronounced reduction in medial PFC and enhaced activation in lateral PFC and vescor-somatic areas.
Slagter et al [32]	2008	EEG	Vipassana	17 subjects, 23 controls (matched for gender, age, and eduacation); 3 months longitudinal study assessing spectral EEG of attentional blink	Trait	Attention	Decreased cross-trial variability was found in the phase of oscillatory theta acitivity after succesful detection of the second of two temporally close targets for meditators compared to controls. This decrease was most pronounced for individuals who showed the greatest reduction in brain resource allocation to the first target. No differences were found in baseline oscillatory activity.
Holzel et al [48]	2008	MRI	Vipassana	20 subjects, 20 controls (matched for gender, age, education, and handedness); cross-sectional study assessing gray matter concentration	Trait	Consciousness & Emotion	Gray matter concentration for meditators was increased in right hippocampus and right anterior insula and showed a trend towards significance for the left inferior temporal gyrus. Gray matter concentration in left ITG correlated with amount of meditation practice and showed a trend towards significance for right insula. Exploratory whole brain analyses revealed a correlation between gray matter concentration in OFC and amount of meditation practice.

Authors	Year	Method	Meditation style	Experimental design	State or trait effect	Domain	Main findings
Lutz et al [47]	2008	fMRI	Tibetan Buddhist - compassion	15 subjects, 15 controls (matched for age); cross-sectional study assessing brain activation in response to emotional sounds during meditation and control condition	State	Emotion	All participants showed increased activation to emotional sounds in anterior insula and ACC during meditation compared to rest and activity in insular cortex was associated with the depth of meditation. Expert meditators exhibit greater insula activation than controls and also showed greated insula activation in reponse to emotional stimuli than neutral stimuli. Experts also showed increased actiation in amygdala, TPJ, and posterior temporal sulcus compared to controls.
van den Hurk [40]	2009	Behavioral	Mindfulness meditation - concentrative & insight	20 subjects, 20 controls (matched for gender and age); cross-sectional design assessing performance on ANT	Trait	Attention	Expert meditators showed increased orienting and executive attention compared to controls. Expert meditators also showed a reduction in error rates compared to controls, when identical reaction times were considered.
Lutz et al [35]	2009	EEG	Vipassana & Metta (compassion)	17 subjects, 23 controls (matched for gender, age, and education); 3 months longitudinal study assessing spectral EEG of performance on dichotic listening task during mediation	Trait	Attention	Reduced variability in attentional processing of target tones was found in meditators as showed by enhanced theta-band phase consistency of oscillatory nearal activity over anterior brain areas and reduced response time variability. This enhanced theta phase consistency was most pronounced for individuals who showed the largest decrease in response time variability.
Cahn & Polich [34]	2009	ERP	Vipassana	16 subjects, no controls; assessment of auditory oddball effects during meditation and control condition	State	Attention	Decreases in ERP components indexing perception and attentional engagement processes were found in response to unexpected stimuli during meditation. Reduction of the P3a amplitude was strongest in meditators with more hours of daily practice and was not evident in meditators reporting drowsiness during the experimental meditation period.
Baijal & Srinivasan [36]	2010	EEG	Sudarshan Kriya Yoga - concentrative	10 subjects, 10 controls (matched for gender and age);	Trait	Attention	Meditators showed increased relative theta power and theta coherence in frontal areas, decreased relative theta power in parietal regions, and decreased absolute alpha power during meditation compared to relaxation of controls. Differences in relative theta power were found only during the deep middle stages of meditation.
Zeidan et al [39]	2010	Behavioral	Mindfulness meditation - concentrative & insight	24 subject, 25 controls (both randomly assigned); 4 day longitudinal study assessing different forms of memory and attention and emotion	Trait	Attention & Emotion	Brief mindfulness training improved visuo-spatial processing, working memory, and executive funitoning and reduced fatigue and anxiety. No differences between the experimental and control condition were found on mood.
Cahn et al [60]	2010	EEG	Vipassana	16 subjects, no controls; assessment of spectral EEG during meditation and control condition	State	Consciousness	Meditation compared to the control condition revealed a decrease in frontal delta power, increased parieto-occipital gamma power, and a relative incerease in frontal theta power. The change in delta power was most pronounced for individuals that reported less drowsiness. Alpha power was correlated with condition order and tended to be correlated with experience and with drowsiness
Travis et al [9]	2010	EEG	TM	19 subjects, 19 controls (both randomly assigned); 10 week longitudinal study assessing changes in EEG power, coherence, and source localization	Trait	Consciousness	TM compared to rest was shown to increase alpha power in frontal regions and to decrease beta and gamma power in frontal regions and log-power in parietal regions. Coherence was shown to increase in frontal areas in alpha and beta ranges. Source localization revealed midline circuits overlapping with the default-mode network.
Holzel et al [49]	2010	MRI	MBSR	26 subjects, no controls; 8 week longitudinal study assessing changes in gray matter concentration	Trait	Emotion	MBSR training revealed a decrease in self-reported stress which correlated with a decrease in gray matter concentration in the basolateral amygdala, though no main effect of the training was found.
Holzel et al [50]	2011	MRI	MBSR	16 subjects, 17 controls (matched for gender, age, ethnicity, and education); 8 week longitundal study assessing changes in gray matter concentration	Trait	Emotion & Consciousness	ROI analyses revealed increases in gray matter concentration in hippocampus of meditators compared to controls but no differences in insula. Exploratory analyses further revealed increases in posterior cingulate cortex, tempo-parietal junction, and cerebellum.