



Neuromodulation and meditation: A review and synthesis toward promoting well-being and understanding consciousness and brain

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ABSTRACT

The neuroscience of meditation is providing insight into meditation's beneficial effects on well-being and informing understanding of consciousness. However, further research is needed to explicate mechanisms linking brain activity and meditation. Non-invasive brain stimulation (NIBS) presents a promising approach for causally investigating neural mechanisms of meditation. Prior NIBS-meditation research has predominantly targeted frontal and parietal cortices suggesting that it might be possible to boost the behavioral and neural effects of meditation with NIBS. Moreover, NIBS has revealed distinct neural signatures in long-term meditators. Nonetheless, methodological variations in NIBS-meditation research contributes to challenges for definitive interpretation of previous results. Future NIBS studies should further investigate core substrates of meditation, including specific brain networks and oscillations, and causal neural mechanisms of advanced meditation. Overall, NIBS-meditation research holds promise for enhancing meditation-based interventions in support of well-being and resilience in both non-clinical and clinical populations, and for uncovering the brain-mind mechanisms of meditation and consciousness.

1. Introduction

There has been a significant development in the recognition of meditation as a practice to enhance well-being in both non-clinical and clinical contexts, with a notable impact on conditions such as depression, addictive disorders, and pain (i.e., Galante et al., 2023a; Goldberg et al., 2018; Kuyken et al., 2016). Meditation-based interventions, including mindfulness-based cognitive therapy (MBCT), are recommended as first-line treatments to prevent depressive relapse, as per the British and Canadian treatment guidelines (National Institute of Health and Care Excellence, 2009; Parikh et al., 2016). Moreover, recent investigations suggest that meditation practices can enhance cognitive functions, such as attention and memory, and potentially serve as a protective measure against age-related cognitive decline from both

healthy aging and conditions such as Alzheimer's disease (AD; Chételat et al., 2017; Gard et al., 2014). Furthermore, in recent years, our understanding of the neuroscience of meditation has significantly grown, and, as such, the neural substrates underlying mental and behavioral changes produced by meditative practices are now better understood. However, our current understanding of meditation remains limited. This is in part due to previous research mainly focusing on clinical aspects rather than mechanistic perspectives, resulting in a scarcity of studies linking the phenomenology of meditation with its neurobiological underpinnings. Further, a significant body of prior research has primarily focused on mindfulness, the most common form of meditation (Tang et al., 2015). However, there exists considerable scope to explore other meditation practices that have received comparatively less attention. These studies, involving long-term meditators and advanced meditation

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practices, offer an exceptional scientific opportunity to investigate significant changes in well-being, explore the associated modifications in states of consciousness, and understand the neural underpinnings behind these processes.

In this review, we explore the neurobiological mechanisms underlying combined neuromodulation and meditation protocols. We focus on previous research that has integrated brain stimulation with meditation practices, specifically those involving neuroimaging or neurophysiological outcomes. We emphasize studies employing combined neuromodulation-meditation interventions in healthy participants to interpret the essential effects of these protocols without confounding factors from pathology. Moreover, we also concentrate on studies with long-term meditators during advanced meditation practices combined with neuromodulation to deepen our understanding of well-being and consciousness states. We argue that uncovering the neural mechanisms of these combined procedures will provide new pathways for fostering subjective well-being across diverse individuals and contexts. The review begins with an overview of our current understanding of the neuroscience of meditation, including a concise discussion of key structural and functional brain features implicated in these practices. We also provide a concise description of the main neuromodulation techniques. Then, in the context of the existing literature, we delve into the integration of brain stimulation techniques with meditation, considering studies where descriptions of the associated neural underpinnings are provided. This examination is then used to propose prospective novel scientific paradigms in meditation research leveraging the use of neuromodulation techniques. These paradigms aim to deepen our understanding of the neural mechanisms of meditation, which is essential for increasing the efficacy of meditation-based interventions.

2. Overview of meditation

Meditation and other contemplative practices, rooted in ancient wisdom traditions and notably those with origins in South Asia, are increasingly becoming the subject of scientific inquiry. Recently, we proposed that meditation research has progressed through two distinct epochs and is now entering a third. The first epoch (approximately 1995–2005) was characterized by foundational studies that demonstrated the therapeutic effects of meditation and began to explore differences between experienced meditators and novices, including initial studies of brain activity. The second epoch (approximately 2005–2020) was marked by more rigorous and mechanistic research, aiming to uncover cognitive-affective mechanisms related to meditation's health benefits. We consider that meditation research is now entering a third phase, focusing on advanced meditation, discussed below (Sacchet et al., 2024). However, before reviewing specific meditation practices, and the current state of the neuroscience of meditation, we first provide an operational definition of the term meditation. We recently proposed that meditation encompasses distinct intentional mental and awareness activities, as observing, focusing, releasing, producing, imagining, and moving (Sparby and Sacchet, 2022). These practices, which can be conducted both in formal and informal settings, are grounded in the foundational practice of being aware of one's own awareness. Accordingly, meditation includes a large family of diverse practices, including mindfulness, mantra meditation, yoga, and tai chi (i.e., Ospina et al., 2007), as well as profound meditative states, for example, the jhanas (Sparby and Sacchet, 2024). To date, scientific research has predominantly focused on mindfulness, the most prevalent form of meditation in Western clinical contexts (e.g., Kabat-Zinn, 1990; 2003; Tang and Posner, 2013; Taren et al., 2015). Mindfulness meditation, sourced from Buddhist contemplative traditions, can be described as a practice centered on maintaining present-moment awareness and acceptance of psychological experiences (Sezer et al., 2022; Tang et al., 2015; Van Dam et al., 2018). Previous investigations have identified distinct behavioral and neurobiological features associated with mindfulness and other meditation practices (e.g., Falcone and Jerram, 2018; Fox

et al., 2014a). Long-term meditators can be conceived of as individuals with substantial meditation practice time, with a range that might vary from many years of experience (i.e., >4 years; Ives-Deliperi et al., 2011) to thousands of hours of practice (e.g., >10,000 h; Lutz et al., 2013). Long-term meditation can lead to profound changes, and can contribute to overall well-being and resilience. However, it's worth noting that not all long-term practitioners—especially those primarily instructed in general meditation techniques, usually mindfulness—have necessarily developed what we call advanced meditation. In this vein, and particularly with growing awareness of the diversity and prevalence of altered states of consciousness, scientific understanding of meditation is expanding beyond basic mindfulness meditation practices (Wright et al., 2024). Advanced meditation encompasses more than the development of basic mindfulness abilities and includes skills, states, and stages that unfold with both time and mastery. This includes transformation of ways of being as well as states and stages of practice that may be characterized by ecstatic bliss, insight into aspects of self and perceptual reality, and altruistic and compassionate experiences (Sacchet et al., 2024). Advanced meditation may evolve in developmental stages (i.e., meditative development) and culminate in specific meditative endpoints, including what has been historically referred to in the Buddhist tradition as 'awakening' or 'enlightenment' (Galante et al., 2023b). It is relevant that motivations and interpretations of these states, stages, and experiences (or their absence) can be rooted in either secular or non-secular frameworks (Sparby and Sacchet, 2022). The science of advanced meditation, meditative development and meditative endpoints promises significant and unique insights into new avenues for further investigating and improving well-being, as well as for exploring the human consciousness processes implicated in them (i.e., Chowdhury et al., 2023; Ganesan et al., 2024; Sparby and Sacchet, 2024; van Lutterveld et al., 2024; Yang et al., 2023; 2024). Notably, Wright et al. (2023) presented a methodological framework aimed at deriving empirically testable hypotheses from wisdom traditions, which might serve as an approach for conducting experimental research on the effects of distinct meditation practices. Of note, while we use a phenomenologically-forward framework for classifying meditation (Sparby and Sacchet, 2022), it is pertinent to consider other definitions and classifications. One leading model is to classify meditation into broad types such as focused attention, open monitoring, and loving-kindness/compassion. Other taxonomies have focused on the cognitive mechanisms of meditation practices, classifying meditation into attentional, constructive, and deconstructive sets of practices (e.g., Brandmeyer et al., 2019; Brewer et al., 2011; Cahn and Polich, 2006; Dahl et al., 2015; Fox et al., 2016; Lutz et al., 2008, 2015). Together, these frameworks can provide meaningful lenses to interpret research findings in the present review. Into the future, as the field of contemplative science continues to mature, it will increasingly explain diverse aspects of meditation, including clinical and non-clinical outcomes of mindfulness and the inherent features associated with its expertise, as well as advanced meditation.

3. Brain structure and meditation

Previous studies have revealed distinct neural correlates of meditation, both at the structural and functional levels of the brain. At the structural level, meditation practices have been linked to specific gray- and white-matter brain features (Fox et al., 2014a; Lazar et al., 2005). Fox et al. (2014a) conducted a systematic review and meta-analysis of 123 morphometric differences, spanning data from 21 neuroimaging studies of around 300 total meditation practitioners. Anatomical likelihood estimation revealed effects on specific brain regions related to meditation. The gray matter regions most consistently associated with meditation practice included the prefrontal (i.e., rostralateral and orbitofrontal), anterior and mid-cingulate, sensorimotor, and insular cortices; the fusiform and inferior temporal gyri; the anterior precuneus; and the hippocampus. These areas are thought to be related to various

phenomenological processes associated to meditation, such as meta-awareness (i.e., prefrontal cortex), exteroceptive and interoceptive body awareness (i.e., sensory cortices), emotion regulation (i.e., cingulate cortex), and memory function (i.e., hippocampus). Additionally, involvement of the corpus callosum and the superior longitudinal fasciculus was also found, showing greater integrity in meditators compared to controls. Notably, a substantial majority of the studies (17 out of 21) examined by Fox et al. (2014a) involved long-term practitioners. In this study, these were defined as meditators who had at least thousands of hours, or several years' worth, of meditation experience. Consequently, it is plausible that the structural findings reported are predominantly influenced by long-term meditation practice. It is also worth acknowledging that this review encompassed a diverse array of meditation modalities, potentially mitigating practice-specific influences, particularly in the context of long-term meditation. Other studies have also highlighted specific structural brain features associated with long-term meditation practitioners (Chételat et al., 2017; Kurth et al., 2015a; Luders et al., 2009). Chételat et al. (2017) observed that elderly long-term meditators exhibited increased gray matter in specific regions of the brain, including the ventromedial prefrontal cortices, anterior cingulate cortex (ACC), and the temporo-parietal junction. As the investigators suggested, given that these effects were particularly evident in brain regions most susceptible to aging and AD, it is tempting to hypothesize that long-term meditation practice may promote brain resilience and maintenance, thus potentially supporting the prevention of age-related cognitive decline. However, recent meditation-based randomized clinical trials (RCTs) have failed to support such a claim despite promoting some behavioral improvements (Chételat et al., 2022). This aligns with large, rigorously conducted RCTs employing mindfulness-based stress reduction (MBSR) interventions, which similarly failed to demonstrate neuroplastic structural changes compared to controls (Kral et al., 2022). Overall, despite previous investigations associating meditation with distinct brain regions including frontal and cingulate cortices, as well as specific subcortical areas, additional research is needed to gain a more comprehensive understanding of how meditation impacts brain integrity, and the potential neuroprotective benefits that meditation-based interventions may offer.

4. Brain function and meditation

In the subsequent section, we provide an overview of key functional brain regions linked to meditation. Prior contributions from notable reviews and meta-analyses shaped this understanding (e.g., Falcone and Jerram, 2018; Fox et al., 2016). Indeed, Fox et al. (2016) conducted a systematic review and meta-analysis of 78 functional neuroimaging studies of meditation. Using activation likelihood estimation, they analyzed 257 peak foci extracted from 31 experiments with a total of 527 participants. They examined four distinct, common forms of meditation: focused attention, mantra recitation, open monitoring, and compassion/loving-kindness. Their findings revealed consistent recruitment within certain brain areas such as the prefrontal cortex (i.e., frontopolar and rostralateral cortices); premotor and supplementary motor area; dorsal anterior and mid-cingulate cortex; and insula during meditation. However, as the authors noted, convergence among meditation types was more of an exception than a rule. Notably, the study found that across all meditation techniques, motor-related regions demonstrated particularly heightened activation. There were also discernible reductions, including the cingulate cortex (posterior division) during focused attention and the thalamus during mantra recitation and open monitoring. Furthermore, results within the same region sometimes exhibited opposite directionality. For example, this pattern was observed in the insula, which increased activity in open monitoring and decreased activity during mantra recitation. However, the authors also highlighted that variability in study designs and differing levels of meditation experience among participants may have influenced the observed results (see for further detail Fox et al., 2016). To overcome

this limitation, Falcone and Jerram (2018) conducted a functional magnetic resonance imaging (fMRI) meta-analysis contrasting mindfulness meditation with a baseline control condition in 21 studies, encompassing a total of 22 contrasts of both novice (11 contrasts) and experienced (12 contrasts) meditators to delineate how brain activity during meditation is influenced by experience. Also using activation likelihood estimation, they found consistent activity across all contrasts associated with mindfulness meditation in the frontal cortex, anterior cingulate region, and insula. Moreover, they observed distinct activation patterns between the novice and experienced meditator groups. In novice participant contrasts, results revealed a significant cluster in the insula. Conversely, in contrasts of experienced meditators, there were significant clusters in the medial frontal gyrus and globus pallidus (Falcone and Jerram, 2018). These functional findings converge on the significance of distinct brain areas in meditation, including frontal, cingulate and insular regions (Falcone and Jerram, 2018; Fox et al., 2016). Further, these results are topographically consistent with previously reported data at the structural brain level (e.g., Chételat et al., 2017; Fox et al., 2014a).

5. Brain networks and meditation

The findings discussed in the prior sections highlight the structural and functional significance of singular brain regions in meditation. These findings exhibit substantial convergence across diverse brain areas—notably, as stated, the frontal cortex, cingulate regions, and insula. These brain regions, however, do not operate in isolation; rather, they are components of distinct neural networks, including the default-mode network (DMN), the salience network (SN), the fronto-parietal network (FPN), and the cortico-limbic circuit. These brain networks might be involved in meditation-related processes such as self-awareness (i.e., DMN); attentional and cognitive control (i.e., SN and FPN); and emotional regulation (i.e., cortico-limbic system). In the subsequent section, we provide a detailed examination centered on these brain networks. Initially, we will explore the functional patterns 'within' these brain networks associated with meditation (i.e., Brewer et al., 2011; Hölzel et al., 2007). Subsequently, we will analyze the dynamic interactions occurring 'between' distinct brain networks linked to meditation, mainly following the findings outlined in a previous publication from our group (Sezer et al., 2022). We will describe interventional studies employing mindfulness meditation, as well as research conducted on long-term practitioners and/or during advanced meditative states.

A consistent neural feature associated with meditation involves specific activity and connectivity patterns within the DMN. The DMN is comprised of nodes including the medial prefrontal cortex (mPFC), precuneus (PCU)/posterior cingulate cortex (PCC), lateral inferior parietal lobes (IPLs), temporal nodes, and the hippocampal formation (Alves et al., 2019; Buckner et al., 2008). The functioning of this brain network, which has been largely explored in resting-state fMRI studies, exhibits negative correlation with brain areas traditionally related to task responses, such as those entailing the FPN (Eryilmaz et al., 2020; Pfefferbaum et al., 2011). The DMN has been associated with self-referential processing, mind wandering, autobiographic memory, and mental time traveling (Addis et al., 2007; Buckner et al., 2008; Mason et al., 2007; Mittner et al., 2016). Meditation practice has been associated with a reduction in activity in certain areas of the DMN, particularly its posterior parietal nodes (i.e., Berkovich-Ohana et al., 2016a; 2016b; Farb et al., 2007; Fujino et al., 2018; Garrison et al., 2015; Kral et al., 2019; Smigielski et al., 2019; Taylor et al., 2013). Moreover, prior significant research conducted on long-term meditators has reported, at the phenomenological level, less mind wandering during meditation sessions compared to meditation-naïve controls (Brewer et al., 2011). At the neural level, authors also revealed that there is a significant reduction in brain activity within core regions of the DMN during meditation, especially in the mPFC and the PCU/PCC, among

these long-term practitioners (Brewer et al., 2011). Another brain network implicated in meditation practice is the SN. This network mainly includes bilateral temporal/insular and ACC regions (Menon and Uddin, 2010; Seeley et al., 2007; Seeley, 2019). This network is important for attention-related processes, cognitive control, and response inhibition (Dosenbach et al., 2010; Menon and Uddin, 2010). This system is believed to facilitate the switching between the anti-correlated DMN and FPN (i.e., see Menon and Uddin, 2010). This switch role of the SN is considered essential for optimal brain functioning (Miller et al., 2008; Spreng et al., 2016). In meditation studies, increased activity and connectivity among SN nodes have been found as a recurring phenomenon linked to meditation (Farb et al., 2013; Lutz et al., 2008; Tang et al., 2010). Hölzel et al. (2007) found that long-term meditators displayed, among other processes, heightened activity in the rostral ACC when compared to a control group during meditation practice. The investigators hypothesized that increased ACC activity in long-term meditators might underlie a heightened capacity for processing distracting events compared to meditation naïve individuals. Furthermore, it is important to consider the FPN's implications in cognitive processes linked to meditation. Including the dorsolateral prefrontal cortex (DLPFC) and postero-lateral parietal regions, this network has been widely implicated in executive functioning and cognitive control processes (Corbetta and Shulman, 2002; Dixon et al., 2018; Seeley et al., 2007). Within the meditation framework, this brain system is believed to facilitate mindful, present-moment interactions with the environment (Hasenkamp et al., 2012; Kajimura et al., 2020; Taren et al., 2017; Vago and Zeidan, 2016). Interestingly, Brefczynski-Lewis et al. (2007) noted that, compared to novices, long-term meditators exhibited heightened activation during meditation within fronto-parietal regions. Additional insights into the implications of this network are detailed in the next section ('Brain oscillations and meditation'). Finally, it is hypothesized that meditation might also modulate the cortico-limbic circuitry, which is crucial to emotion regulation. This brain network mostly includes largely interconnected structures such as the hippocampus and amygdala, among others (i.e., septal nuclei; Chow et al., 2018; Fuchs and Flügge, 2003). Within meditation research, amygdala activity reductions have been observed both in response to meditation-based interventions in naïve-meditation individuals (i.e., Goldin and Gross, 2010; Taren et al., 2015) as well as in long-term meditators (i.e., Brefczynski-Lewis et al., 2007). In this context, Brefczynski-Lewis et al. (2007) observed reduced amygdala activation related to emotional distractors in long-term practitioners compared to novices. Furthermore, they also observed a negative correlation between hours of meditation practice and amygdala activation, suggesting that extended meditation practice may facilitate—possibly via neuroplastic effects—top-down inhibitory processes. Therefore, there appears to be a distinctive pattern in the dynamics of these brain networks. Specifically, the DMN and cortico-limbic circuitry mainly show reduced activity and connectivity associated with meditation, which may underlie decreased self-referential processing and emotional reactivity. Conversely, specific increases in the FPN and SN have been observed in the context of meditation, which might underlie enhanced attentional and cognitive control processes.

In addition to specific within-network activity and connectivity patterns, it has also been emphasized how phenomenological processes tied to meditation, such as self-awareness, attention control, and emotion regulation, might be particularly associated with between-network dynamics. In a previous review of functional connectivity in mindfulness meditation, Sezer et al. (2022) observed that meditation-related changes in self-awareness are linked to decreased connectivity between the SN and the cuneus. Additionally, attention control during meditation seems to be associated with increased connectivity between the PCC (within the DMN) and the DLPFC (within the FPN). Furthermore, emotion regulation in the context of meditation correlates with increased connectivity between the rostral ACC (rACC) and the dorsomedial prefrontal cortex (a core DMN region), as well as

between the rACC and the amygdala (a region of the limbic system). These results are in line with recent findings suggesting that increased between-network connectivity is a crucial neural underpinning of meditation, particularly among long-term practitioners. In this vein, Czajko et al. (2023) found increased integration of different large-scale brain circuits, encompassing the somatomotor, dorsal and ventral attention, limbic, and fronto-parietal networks, which may suggest a neural signature of meditation expertise in long-term meditators. Remarkably, this neural signature correlated with a greater ability to generate psychological distance with thoughts and emotions. These data imply that enhanced integration between bodily maps and affective and attentional networks in meditation experts may potentially serve as a hallmark of the embodied cognition fostered by these contemplative disciplines (Czajko et al., 2023). Altogether, this data suggests that understanding the complex neural mechanisms underlying the distinct processes associated with meditation necessitates a thorough examination of both within-network dynamics as well as a detailed analysis of the interactions between these circuits.

6. Brain oscillations and meditation

Complementing insights gleaned from brain imaging studies, electrophysiological data have also significantly enhanced our understanding of the neuroscience of meditation. In a comprehensive systematic review, Lomas et al. (2015) examined the electroencephalography (EEG) correlates of mindfulness meditation, encompassing a total of 56 research articles and comprising data from 1715 subjects (1358 healthy individuals and 357 psychiatric patients). The results indicated that mindfulness practices predominantly exhibit increases in alpha and theta power compared to resting state, while no consistent trends were observed regarding beta, delta, and gamma bands in relation to mindfulness. Regarding advanced meditation practices in long-term meditators, Lutz et al. (2004) observed in an early EEG-meditation study that experienced meditators could voluntarily induce pronounced gamma-band oscillations and synchronized brain rhythms during meditation, differing markedly from non-experienced meditators, especially in the lateral fronto-parietal brain regions. Moreover, these practitioners exhibited an elevated ratio of gamma-band (25–42 Hz) to slower (4–13 Hz) wave activity even before engaging in meditation, predominantly at the medial fronto-parietal electrodes. This dissimilarity was amplified significantly throughout the meditation session across numerous scalp areas and persisted even post-meditation, signifying the enduring effects of long-term meditation on brain dynamics. Furthermore, the duration of meditation training correlated with a higher proportion of relative gamma activity, implying that this practice may trigger mechanisms of brain plasticity. In a more recent EEG study, Yordanova et al. (2021) investigated how meditation practice impacts cognitive control brain systems, focusing on the synchronization of fronto-parietal and medial-frontal circuits. In this investigation, highly experienced and novice meditators were studied during different meditation styles (focused attention, open monitoring, and loving-kindness). Results showed that compared to novice meditators, experienced meditators exhibited strong theta synchronization of both fronto-parietal and medial-frontal networks in left parietal regions across all meditation styles; and only the connectivity of lateralized beta medial-frontal networks varied between meditation styles. Moreover, intra-hemispheric theta fronto-parietal connectivity showed non-linear dependence on expertise, while inter-hemispheric fronto-parietal connectivity in faster frequency bands increased linearly with meditation expertise. In summary, previous results indicate, at the neurophysiological level, a prominent role of alpha and theta frequencies in mindfulness meditation, with gamma being particularly associated with long-term meditators. Furthermore, specific frequencies seem to be sensitive to meditation practice (e.g., theta) and meditation modality (e.g., beta). At the topographical level, this data reinforces the central role that fronto-parietal control systems appear to play in meditation.

7. Caveats and limitations in our understanding of the neural basis of meditation

Despite the considerable development in the neuroscience of meditation, significant limitations remain. At the structural level, association of meditation with distinct areas linked to the DMN, including the PCC/PCU, is not completely consistent. For instance, [Yang et al. \(2019\)](#) found that cortical thickness in the precuneus increased after 40 days of mindfulness meditation training. This is also consistent with data reported in previous reviews (i.e., [Fox et al., 2014a](#)). However, [Kang et al. \(2013\)](#) revealed an antero-posterior structural dissociation when comparing meditators with controls, with greater cortical thickness in the anterior areas of the brain and thinner cortex in the posterior regions, including the PCC. Similarly, [Berkovich-Ohana et al. \(2020\)](#) observed reduced gray matter density in the precuneus region associated with prolonged meditation practice. Others, such as [Grant et al. \(2013\)](#), have not been able to detect any discernible structural differences related to meditation in these posterior nodes of the DMN. At the functional level, a consistent observation in meditation research is a decrease in activity within DMN nodes ([Berkovich-Ohana et al., 2016a; 2016b; Brewer et al., 2011; Farb et al., 2007; Ives-Deliperi et al., 2011; Pagnoni et al., 2008; Pagnoni, 2012](#)). However, the precise nature of these DMN-related functional brain changes, as well as distinctions related to factors such as meditation experience and types of practice, remains ambiguous (e.g., [Jang et al., 2011; Taylor et al., 2013; Xu et al., 2014](#)). Similarly, how meditation experience modulates affective cortico-limbic pathways is uncertain (i.e., [Taylor et al., 2011](#)). Previous studies have also observed distinct neural oscillatory patterns associated with meditation in the fronto-parietal circuit. Specifically, there are apparent disparities when comparing mindfulness meditation ([Lomas et al., 2015](#)) with long-term meditators during advanced meditation ([Lutz et al., 2004](#)), as well as when analyzing data considering long-term practitioners (i.e., [Lutz et al., 2004; Yordanova et al., 2021](#)). These differential—and occasionally contradictory—findings highlight the need for more replicable research. They also emphasize the importance of adopting innovative methodological approaches to reveal mechanisms and causal dependencies of these brain features on distinct meditative practices.

Numerous methodological issues may account for the observed discrepancies in previous neuroimaging and neurophysiological findings related to meditation. Level of meditation expertise is an important inclusion criterion to consider for meditation research. Including meditators with diverse levels of meditative expertise may introduce challenges in interpreting the results of certain investigations (i.e., [Falcone and Jerram, 2018; Fox et al., 2016](#)), as it becomes unclear whether the observed effects are primarily due to processes associated with the learning of a new (unspecific) practice or are due to specific changes associated with meditation practice. Other methodological limitations in previous meditation research literature include small sample sizes, heterogeneous “sham” meditation conditions, and infrequently conducted power analyses (i.e., [Davies et al., 2021; Zeidan et al., 2015](#); for further related empirical discussion, see also [Goldberg et al., 2022](#)). Also of note, some have expressed concerns about the usefulness of specific paradigms as true controls for meditative practices. This is because meditation not only modifies brain function during the practice itself but also leads to persistent changes in neural dynamics (i.e., [Lutz et al., 2004](#)). Therefore, typical resting-state control conditions may not be suitable for accurate comparisons in meditation research. It is worth noticing here, nonetheless, that recent neuroimaging studies on meditation are overcoming this limitation by using non-meditative control tasks instead of resting state as control conditions ([Yang et al., 2023](#)).

Another important methodological concern arises from the frequent reliance on cross-sectional and correlational data to understand the neural basis of meditation, which inherently limits our ability to make causal attributions about the effects of meditation. In cross-sectional observational studies, previous investigations have focused on

identifying associations between meditation experience (i.e., measured in estimated hours of practice) and diverse structural and functional brain features. Some of these efforts aim to infer causation-like assumptions about changes in the brain resulting from meditation. However, it is also plausible that pre-existing differences in specific brain characteristics could be influencing these associations. A viable strategy to mitigate limitations associated with single time-point observations is in adopting longitudinal methodologies, which can offer better insights into causality. However, when these procedures have been implemented in the meditation context, they have often encompassed relatively short time periods, resulting in limited effects (with durations of days to several weeks; refer to [Tang et al., 2015](#) for further debate).

Non-invasive brain stimulation (NIBS) methodologies have the potential to effectively address some of these concerns. These techniques, most commonly involving the use of brief magnetic fields and subtle electrical currents, enable the modulation of brain activity in a precise and safe manner. Importantly, they hold significant potential as tools to both increase or decrease brain activity externally, depending on the parameters used (e.g., [Rossini et al., 2015](#)). Hence, these methods have been used to restore the normal function of distinct brain features in different clinical contexts, including depression and obsessive-compulsive disorder ([Blumberger et al., 2018; Cohen et al., 2022](#)). Moreover, these techniques can also be experimentally applied to temporarily alter the functioning of a specific brain region or network. These latter research procedures, known as perturbational (or virtual lesion) approaches (i.e., [Pascual-Leone et al., 2000; Walsh et al., 2006](#)), allow for causal inferences, revealing the necessity of a given brain process for a specific mental or behavioral function. Hence, these perturbational approaches might allow for overcoming the intrinsic limitations of correlational data, providing a more accurate mechanistic understanding of brain-behavior associations.

8. Fundamentals of electromagnetic neuromodulation techniques

Before reviewing the current research applications of non-invasive neuromodulation techniques in influencing neural patterns associated with meditation, it is essential to briefly outline the principles behind these methods. Presently, transcranial magnetic stimulation (TMS) and transcranial electrical stimulation (tES) are widely regarded as the predominant techniques in the NIBS field.

TMS is a technique that utilizes Faraday’s principle of electromagnetic induction to modulate the brain non-invasively. This principle states that the transmission of a large, brief pulse of current through loops of copper wire (i.e., magnetic coil) gives rise to a fluctuating magnetic field perpendicular to the plane of the coil. This magnetic field subsequently induces an electric field predominantly parallel to the inner surface of the volume conductor adjacent to the coil. If the coil is held over the subject’s head, the magnetic field pulse penetrates the scalp and skull largely unimpeded, reaching the brain where an electric field is induced that can produce neuronal firing in the targeted area and modulate neural excitability ([Eldaief et al., 2013; Huerta and Volpe, 2009; Ridding and Rothwell, 2007](#)). When TMS is administered to the motor cortex, it triggers a cascade of cortico-spinal descending waves that sum up at the spinal segmental level, depolarize alpha motor neurons, and can induce muscle contraction. This muscular response, which can be quantified through electromyography (EMG), is known as a motor evoked potential (MEP). This method is routinely used to determine individual stimulation intensities in TMS procedures. When applied over non-motor areas, TMS-induced field potentials can be recorded using EEG ([Farzan et al., 2016; Ozdemir et al., 2020](#)). Furthermore, TMS also exerts distributed brain network effects that can be precisely captured with the concomitant use of fMRI (e.g., [Abellana-Pérez et al., 2019; Pascual-Leone et al., 2011](#)). TMS protocols can be administered in various formats: single, paired, or with repetitive burst sequences. Initial applications of single-pulse TMS primarily

centered on exploring central motor conduction pathways and facilitating the mapping of functional territories within the sensorimotor system (Hallett, 2007). The evolution to paired-pulse protocols, including strategies such as paired associative stimulation (PAS), has paved the way for more in-depth investigations into cortical physiology. These protocols permit the exploration of functional relationships either within a specific brain region or between two interconnected areas, offering a powerful approach to study cortical interactions (Dayan et al., 2013; Reis et al., 2008; Wassermann et al., 2008). Repetitive TMS (rTMS) encompasses a wide range of TMS methods. The 'classical' form of rTMS is defined by trains of individual TMS pulses delivered at a constant frequency and intensity. These rTMS protocols can increase or decrease cortical excitability, the specific outcome of which is contingent upon distinct stimulation parameters including duration, stimulus frequency, and intensity of pulses (Fregni and Pascual-Leone, 2007; Hallett, 2007). In general, high-frequency rTMS tends to enhance cortical excitability (Peinemann et al., 2004), while low-frequency rTMS tends to diminish it (Muellbacher et al., 2000). However, notable inter- and intra-individual variability in response to TMS protocols has been observed (i.e., Hamada et al., 2013; Maeda et al., 2000; 2002; Perellón-Alfonso et al., 2018). The underlying synaptic mechanisms responsible for lasting effects observed with rTMS relate to neuroplasticity processes known as long-term potentiation (LTP) and long-term depression (LTD; Cooke and Bliss, 2006). As such, 'patterned' rTMS protocols, such as theta-burst stimulation (TBS; Huang et al., 2005), employ bursts of high-frequency stimulation (3 pulses at 50 Hz repeated at 200 ms intervals) that can be applied intermittently (iTBS) or continuously (cTBS) to directly induce LTP- and LTD-like processes (Di Lazzaro et al., 2008; Huang et al., 2005). In clinical practice, single and paired pulses have primarily found utility for diagnostic purposes (Benussi et al., 2017; 2020; Conte et al., 2009; Padovani et al., 2018). In contrast, repetitive pulses have predominantly been used to explore causal relations between brain activity and behavior (Pascual-Leone et al., 2000) and for neuromodulation treatment (Blumberger et al., 2018; see also Burke et al., 2019 for further detail).

tES is another broadly employed NIBS technique. tES really represents a group of methods that produce their neural effects by generating weak electrical currents that are applied to the scalp resulting in 'faradizing' of the brain or modulation of specific brain oscillations. Transcranial direct current stimulation (tDCS) and transcranial alternating current stimulation (tACS) represent the most prevalent tES methods. Other techniques, such as transcranial random noise stimulation (trNS), are also included within this domain. The mechanism of action of tDCS involves the depolarization of neural membrane potentials under the anode, thereby resulting in increased cortical excitability. Conversely, under the cathode, neural membrane potentials undergo hyperpolarization, which diminishes cortical excitability (Lefaucheur and Wendling, 2019; Nitsche and Paulus, 2000; Nitsche et al., 2008; Purpura and McMurtry, 1965). tACS administers a sinusoidal current to the scalp at specific frequencies, thereby facilitating an exogenous modulation of ongoing brain oscillations (Ali et al., 2013; Antal and Herrmann, 2016; Antal and Paulus, 2013; Herrmann et al., 2013; Moisa et al., 2016; Reato et al., 2013; Wischniewski et al., 2023). Beyond their immediate effects, both tDCS and tACS techniques exhibit enduring after-effects that outlast the duration of the stimulation, likely as a result of fostering neuroplasticity processes or the entrainment of specific oscillations (Kasten et al., 2016; Liebetanz et al., 2002; Monte-Silva et al., 2013; Nitsche and Paulus, 2001; Nitsche et al., 2003; Vossen et al., 2015; Wischniewski et al., 2019). Individual variability in tES responses has also been observed (i.e. López-Alonso et al., 2014). Recent advancements, primarily using direct current stimulation, have led to the development of innovative procedures to concurrently stimulate multiple regions of the brain. With the goal to comprehensively target large-scale brain circuits, these approaches are called multifocal or network-based tES protocols (Abellana-Pérez et al., 2021; Fischer et al., 2017; Lindenberg et al., 2010; Ruffini et al., 2014; Vaqué-Alcázar

et al., 2021). It should be noted that, similar to tES, TMS procedures can also be applied using multifocal assemblies (Jiang et al., 2013; Ruohonen and Ilmoniemi, 1998).

NIBS protocols are increasingly integrated into both clinical and research settings. The U.S. Food and Drug Administration has officially endorsed specific TMS protocols for the treatment of certain neuropsychiatric conditions (Blumberger et al., 2018; Cohen et al., 2022). However, no tES protocols have currently secured clinical approval. Beyond clinical applications, NIBS procedures have also gained significant interest in research settings due to their unique capacity in human neuroscience to deepen our understanding of the brain. Hence, while neuroimaging technologies have facilitated the study of structural and functional brain correlates of differential mental functions, establishing these correlative links does not unequivocally imply that a measured brain process is necessary or sufficient for a specific mental or behavioral process. Consequently, a growing number of studies have leveraged NIBS techniques to experimentally test brain-behavioral associations in scientific studies. In these scenarios, and particularly when utilizing perturbational approaches, researchers can infer a causal connection between a specific behavioral process and a given brain feature.

9. Recent advancements in neuromodulation and meditation studies

We will focus on studies conducted in healthy participants. However, the integration of brain stimulation with meditation has also been explored in the context of neuropsychiatric conditions. While this topic extends beyond the primary focus of this article, it is pertinent to mention that some studies, particularly using tES, have yielded remarkable neurobiological insights, which can be explored in detail in the works of Ahn et al. (2019), Pollonini et al. (2020), or Park et al. (2021). However, as previously indicated, elucidating the fundamental neural mechanisms of integrating meditation with neuromodulation within the context of neuropsychiatric conditions is challenging given the complex neurobiological nature of these conditions. The data described below is also summarized in Table 1. Additionally, Fig. 1 provides details on the methodological aspects, while Fig. 2 presents the main observed results.

9.1. tES

We provide here a review of initial insights from studies that have employed NIBS in meditation research, focusing on those reporting both its behavioral and neurobiological effects. We synthesize the main outcomes of these investigations focusing on those principally linked to the combined protocols. First, we will examine studies employing tES due to its most frequent integration in preceding meditation studies. The prevalent use of tES in meditation research is underscored by recent reviews by Rebello-Sanchez et al. (2022) and Divarco et al. (2023). These reviews detail results from studies employing tDCS alongside meditation, aiming to enhance the behavioral effects of meditation-based interventions in both non-clinical and distinct clinical settings. Most studies used tDCS with the anode placed over frontal areas (i.e., Nishida et al., 2021), while fewer have focused on other brain regions (i.e., Park et al., 2021). Mindfulness meditation was the predominant category of meditation reported in the reviewed studies [i.e., in their review, Divarco et al. (2023) noted that mindfulness was the meditation modality of 15 out of the 20 published investigations (75 %) and 12 out of the 13 ongoing studies (92 %)]. Moreover, there was substantial variability in the neuromodulation protocols of reviewed studies, including, among others, differences in the number and duration of tDCS sessions. A significant number of investigations showed positive behavioral and clinical outcomes from combining electrical stimulation with meditation, despite a particular instance where symptoms appeared to worsen (Clarke et al., 2020). However, only a

Table 1

Summary of the principal methodological characteristics and main outcomes of the included studies. The table provides information on study design, NIBS protocols and targets, meditation procedures, participants, behavioral results, neural outcomes, and main implications. For participants, the initial sample size is reported, with the final sample size indicated in parentheses if different.

Study	Study design	NIBS protocol and targets	Meditation procedure(s)	Participants	Behavioral results	Neural outcomes	Main implications
Hunter et al. (2018)	Randomized, double-blind, parallel.	tDCS: 2 mA for 30 min. Anode: rIFG (F10). Cathode: Left upper-arm.	Mindfulness-based training.	34 (29) healthy individuals. Active tDCS: n = 17 (16). Sham tDCS: n = 17 (13).	Active tDCS, but not sham, revealed an increase in cognitive performance (working memory).	Active tDCS, compared to sham, displayed decreased frontal and increased parietal P3 amplitude and theta power. Cognitive performance gains correlated with increased parietal theta power in the active tDCS group.	Neural modulations sustaining cognitive improvements in the active tDCS group were elucidated within the neural efficiency hypothesis.
Nishida et al. (2021)	Randomized, double-blind, parallel.	tDCS: 1 mA for 20 min. Anode: L-DLPFC (F5). Cathode: Left shoulder.	Treadmill walking for focused mindfulness.	58 (54) healthy individuals. Active tDCS: n = 28 (26). Sham tDCS: n = 30 (28).	In the active tDCS group, STAI-S was reduced 1-week post-intervention as compared to sham.	In the active tDCS group, current density of alpha activity in the L-DLPFC and rACC was reduced, compared to sham. In the active tDCS group, modulations in rACC alpha density were associated with STAI-T changes at 1-week.	The inclusion of neuromodulation might have amplified the effects of meditation on behavior and brain activity. Reported neural patterns may provide insights into the mechanisms underlying behavioral changes linked to the intervention.
Sefat et al. (2022)	Randomized double-blind, cross-over.	tDCS: 2 mA for 20 min. Anode: L-DLPFC (F3). Cathode: R-DLPFC (F4).	Hatha yoga.	22 (18) healthy individuals.	Unreported.	Active tDCS condition revealed increased functional connectivity mostly comprising the frontal region. At the source level, these modulations were mainly found within the fronto-parietal circuit.	Incorporating neuromodulation into yoga practice could potentially amplify changes at the brain network level, especially in those associated with executive domains.
Bodart et al. (2018)	Case study.	Single-pulse TMS. TMS was applied targeting a frontal and a parietal region in the left hemisphere.	Open presence meditation; self-induced cognitive opacity; closed-eye drowsy state.	A 69-year-old, left-handed, long-term Tibetan Buddhist meditator.	Unreported.	The three different self-induced mental states selectively modulated cortical reactivity and connectivity metrics in a target-specific manner.	The neural differences observed in frontal and parietal targets may be attributed to the phenomenological features of each self-induced mental state.
Gosseries et al. (2020)	Case study.	Single-pulse TMS. TMS was applied targeting a frontal and a parietal region in the right hemisphere.	Cognitive trance from shamanic traditional practice.	A 56-year-old, right-handed, female, with long-term experience in shamanistic trance.	Self-reported measures of wakefulness, absorption, dissociation, and time perception were more pronounced during trance compared to rest, particularly for the parietal target.	Neurophysiological explored metrics were heightened during cognitive trance when stimulation was applied to the frontal region, as compared to the resting state. Conversely, most indicators showed a decrease during parietal stimulation.	The increased frontal neural responses might be associated to shifts in processes such as attention and internal monitoring, while the reduced parietal responses could be linked to lower awareness of the environment during cognitive trance.
Luo et al. (2023)	Randomized single-blind, cross-over.	rTMS (iTBS). Target: L-DLPFC (F3).	Engagement in self-compassion.	32 healthy individuals.	An increase in self-compassion was observed when participants underwent iTBS compared to sham.	iTBS led to increased gamma band power and coherence, which correlated with engagement in self-compassion. Theta activity was distinctly modulated based on the social context (self-compassion and social rejection).	The findings suggest that the DLPFC is relevant in shaping self-compassion, with mostly gamma activity being associated with it.

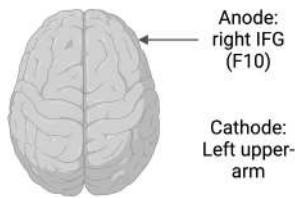
limited number of studies concomitantly reported the putative neural mechanisms underlying the behavioral effects associated with these combined protocols in healthy individuals.

Hunter et al. (2018) implemented a protocol of 4-week mindfulness-based training (MBT) coupled with tDCS applied to the right inferior frontal gyrus (rIFG) in a healthy adult sample, hypothesizing that this combined intervention may aid in enhancing cognitive performance (i.e., working memory). Thirty-four healthy participants

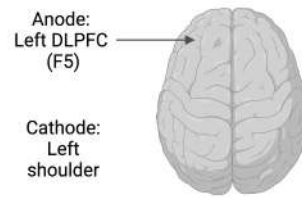
were assigned randomly to one of two groups: a MBT group receiving tDCS (n = 17), or an active control group undergoing sham stimulation (n = 17). Specifically, the anode electrode was positioned over F10, according to 10/10 International system. The cathode was situated over the contralateral upper-arm. Stimulation was delivered at 2 mA for 30 min. At the behavioral level, the MBT-tDCS group, but not the control group, showed enhanced cognitive performance in the 3-back task and the spatial span task (used as a transfer task). At the neural level,

A) Combined tDCS-meditation research

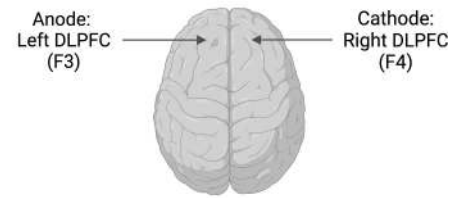
A.1) tDCS and MBT



A.2) tDCS and TW-FM

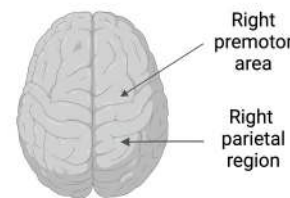
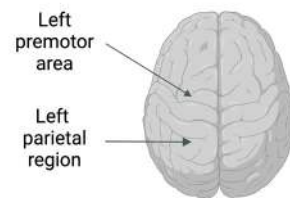


A.3) tDCS and Hatha yoga



B) Combined TMS-meditation research

B.1) Single-pulse TMS in long-term meditators



B.2) rTMS and self-compassion

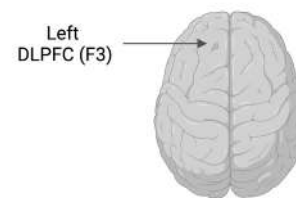
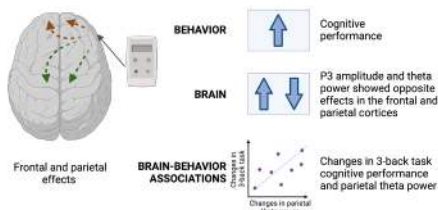


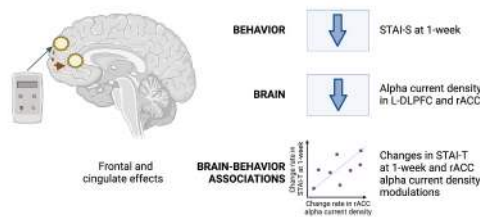
Fig. 1. Synthesis of the stimulation techniques and meditation practices used in the reviewed studies. A) Combined tDCS and meditation protocols utilized in the included investigations. B) Combined TMS and meditation procedures employed in the studies examined. Note: Black arrows pointing at brain templates indicate an approximation of the center of stimulation targets in both tDCS and TMS studies. The figure was generated using BioRender.com.

A) Combined tDCS-meditation research

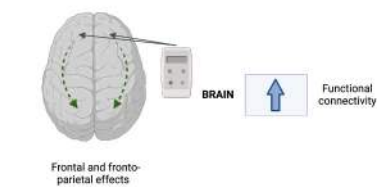
A.1) tDCS and MBT



A.2) tDCS and TW-FM

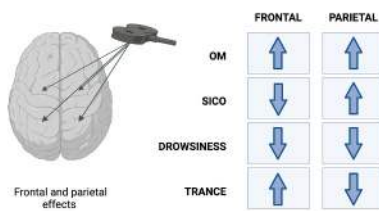


A.3) tDCS and Hatha yoga



B) Combined TMS-meditation research

B.1) Single-pulse TMS in long-term meditators



B.2) rTMS and self-compassion

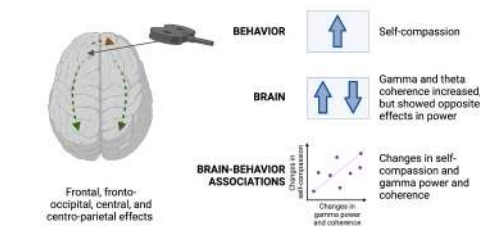


Fig. 2. Summary of the main findings derived from the reviewed articles. A) Insights obtained from combined tDCS and meditation investigations elucidate discernible alterations at both cognitive and affective levels, with neural effects predominantly manifesting in frontal, fronto-parietal, and cingulate regions. Please note that the brain template in section A.2 is primarily intended to illustrate top-down processes. B) Findings from studies combining TMS and meditation unveil distinctive frontal and parietal TMS-EEG signatures linked to various self-induced mental states, alongside specific behavioral and neural effects observed during rTMS application in the context of self-compassion. Note: Blue arrows within the boxes represent changes associated with indicated behavior or neural activity. In brain templates, black arrows indicate an approximation of the center of stimulation targets; green dashed arrows signify heightened brain activity responses; red dashed arrows denote decreased activity. The figure was created using BioRender.com.

individuals in the MBT-tDCS group exhibited heightened P3 amplitude and theta power at the electrode site Pz, accompanied by a concomitant reduction in frontal midline P3 amplitude and theta power during the 3-back task when compared to the control group (i.e., reduction in frontal and increase in parietal activity). Additionally, it was observed that relative increases in Pz theta power were correlated with relative gain scores during the 3-back task in the active tDCS group. Therefore,

the combined neuromodulation and meditation intervention improved cognitive performance accompanied by concurrent frontal and parietal brain modulations. The authors interpreted these brain activity changes underlying cognitive improvements within the context of the neural efficiency hypothesis (Neubauer and Fink, 2009). In general terms, this hypothesis describes that individuals with higher cognitive abilities exhibit reduced neural activation compared to those with lower

cognitive abilities while engaged in identical cognitive tasks (Dunst et al., 2014). In this scenario, hypothetically, neural efficiency could have been enhanced through the synergistic implementation of brain stimulation with meditation, which might explain the improved cognitive performance in active tDCS subjects as compared to control participants.

In another study combining electrical stimulation with neurophysiological data, Nishida et al. (2021) conducted a double-blind randomized study with 58 healthy individuals (active stimulation, $n = 28$; sham stimulation, $n = 30$) to examine anxiety and EEG responses. The intervention combined tDCS applied over the left DLPFC (L-DLPFC; F5), with walking mindfulness, specifically utilizing a method known as treadmill walking for focused mindfulness (TW-FM). Stimulation was administered at 1 mA for a duration of 20 min. In this study, behavioral outcomes linked to anxiety were evaluated using the State-Trait Anxiety Inventory (STAI) before and after the intervention, as well as 1-week post-intervention. Neural responses were quantified through EEG alpha band current density metrics before and after the intervention. At the behavioral level, results revealed that STAI-state (STAI-S) anxiety was reduced 1-week post-intervention in the active stimulation compared to the sham stimulation group. At the neural level, the authors reported that tDCS reduced the current density of alpha activity in the L-DLPFC and rACC as compared to sham post-intervention. Furthermore, modulations in rACC alpha current density after the intervention significantly correlated with 1-week STAI-trait (STAI-T) anxiety changes in the active tDCS group. These results suggest that incorporating neuromodulation could have produced a more significant impact of meditation at both the behavioral and brain levels. Moreover, changes registered in neural activity may help elucidating potential mechanisms underlying the observed effects in behavior resulting from this intervention. Precisely, changes in rACC alpha current density might have mediated the effects on anxiety induced by meditation. This hypothesis is compelling because DLPFC stimulation seems to be able to directly modulate rACC activity (Vink et al., 2018). Further, given the neural connections between the rACC and the amygdala (e.g., Jhang et al., 2018; Shackman et al., 2011), changes in rACC activity might have subsequently affected amygdala dynamics via top-down processes.

In a third study, Sefat et al. (2022) combined yoga (a movement-based meditation practice) with prefrontal tDCS to explore its combined effects using resting-state EEG recordings. Specifically, the intervention employed the Hatha yoga modality. In this study, 22 healthy individuals took part in a cross-over design: on two separate days, participants engaged in either a yoga session combined with active tDCS or a yoga session combined with sham tDCS. During the active tDCS session, a current of 2 mA was applied for 20 min, with the anode positioned at the F3 region (L-DLPFC) and the cathode over the F4 (right DLPFC; R-DLPFC). Changes in power spectral density pre- to post-intervention were not different between the yoga-active tDCS and yoga-sham tDCS conditions. However, the active tDCS condition exhibited increased functional connectivity mainly entailing the frontal region. More precisely, the study identified widespread intra- and inter-hemispheric neural changes characterizing distinct connectivity modulations, primarily between the frontal region and other brain areas. At the source level, these neural changes were predominantly found within the fronto-parietal network. Therefore, adding neuromodulation to yoga practice might enhance brain changes at the network level, particularly to those circuits related to executive processing.

9.2. TMS

Bodart et al. (2018) conducted a study combining TMS and EEG to investigate the modulation of brain reactivity and connectivity during distinct meditative states. The study focused on a 69-year-old, left-handed Tibetan Buddhist long-term meditator (with more than sixty thousand hours of practice). The investigation examined three voluntarily induced mental states: (1) open presence meditation, a

meditative state where the duality of object and subject is diminished; (2) self-induced cognitive opacity (SICO), a mental state where higher cognitive functions are minimized; and (3) a closed-eye drowsy state leading to light sleep. TMS was applied targeting two different sites: (1) the medial parts of the left superior parietal and (2) frontal (premotor area) gyri. They analyzed each mental state using three indices compared to baseline: (1) divergence index (DI), or the percentage of samples that differed significantly across all channels and latencies as an index of overall change in brain response (see Casarotto et al., 2010); (2) power of the target site natural frequency range, which serves as a circuit-specific index of cortical reactivity; and (3) global phase-locking factor (PLF), calculated across all scalp sites as an index of connectivity. Compared to baseline resting state, each self-induced mental state produced a neural modulation significantly larger than the physiological variability of TMS-evoked potentials (TEPs), as revealed by the DI values above empirical cut-off for all three states (see Casarotto et al., 2010). These differences were particularly pronounced for the parietal target for all three mental states. When looking at changes in the power of target site natural oscillation frequency, oscillatory activity was dampened in both parietal (15–25 Hz) and premotor (25–35 Hz) areas during the drowsy state. Conversely, during open presence meditation, there was an enhancement in the power of site-specific evoked oscillations for both parietal and premotor stimulation targets. During the SICO state, there was a target-specific dissociation in cortical reactivity: while the spectral power values remained above baseline resting state during parietal stimulation, they decreased during premotor stimulation below both baseline resting state and even drowsiness state levels. These target-specific reactivity patterns were paralleled in overall connectivity as measured by the global PLF. PLF decreased in both parietal and premotor targets during the drowsy state, while PLF increased in both targets during open presence monitoring. Yet, during the SICO state, PLF was reduced only with premotor target stimulation. The investigators interpreted these induced brain changes suggesting that the heightened cortical reactivity and connectivity indices in both premotor and parietal stimulation targets during open presence meditation might relate to amplified self-awareness and auto-monitoring during this practice. Furthermore, a reduction in the premotor cortex target's TMS neural reactivity and connectivity responses during SICO may relate to decreased engagement of the frontal regions during this state, consistent with a decrease in higher cognitive activity. During the drowsy state, the general decrease in DI, power of evoked oscillations, and global PLF might mirror changes in consciousness across the wake-sleep cycle (Pigorini et al., 2015). In summary, this TMS-EEG approach revealed that different self-induced mental states distinctly modulated cortical reactivity and connectivity metrics in a target-dependent manner. Remarkably, the observed neural differences in frontal and parietal targets might be explained in the context of the phenomenological characteristics of each induced mental state.

In a subsequent TMS-EEG study conducted by the same research group, Gosseries et al. (2020) built upon the findings reported by Bodart et al. (2018) by adapting the previously used TMS-EEG paradigm to investigate cortical reactivity, synchrony, and phase locking during other non-ordinary states of consciousness. They aimed to investigate the neural underpinnings of 'cognitive trance' from shamanic traditional practice as compared to a resting wakefulness state. According to Frecka et al. (2016), shamanic states can be conceived as "a form of focused and expanded consciousness, closer to meditative states, in which the participant intentionally shifts his or her awareness from ordinary perception toward a different 'input', which seems to originate from 'within'" (see also Flor-Henry et al., 2017 for further related theoretical explanations). The case study participant was a 56-year-old right-handed female who completed shamanistic training in Mongolia and practiced trance for 17 years. The stimulation targets were a frontal area (premotor cortex) and a parietal region (posterior parietal cortex) of the right hemisphere. After each TMS-EEG session (i.e., frontal vs. parietal), the participant provided free recall of the subjective

experience and scored time perception (subjective duration of the experience, in minutes), level of arousal (wakefulness), absorption (becoming fully involved in the experience), and dissociation (mental separation from the environment) using 0–10 visual analogue scale (VAS) scores (Vanhaudenhuyse et al., 2019). Compared to rest, at the descriptive phenomenological level, during trance the subject reported feeling more awake ('fully awake' for both sessions during trance vs. 'normal wakefulness' during rest), heightened absorption (8/10 for frontal session and 10/10 for parietal session in trance vs. 6/10 for rest), greater dissociation (8/10 for frontal session and 10/10 for parietal session in trance vs. 0/10 for rest), and a significant distortion in time perception (perceived duration of 8 min for frontal session and 2 min for parietal session in trance vs. 15 min in rest, which was the actual session duration). Overall, self-reported measures of absorption, dissociation, and time-scale distortion were more pronounced during parietal stimulation. Despite the intrinsic challenges of summarizing subjective experience, it is worth noting that the participant managed to integrate the TMS sound into the trance experience during the frontal stimulation session. This integration apparently led to sensations of harmony restoration. Conversely, for the parietal session, the presence of the TMS apparatus was not mentioned, and the participant reported experiences of ecstasy, joy, happiness, and expanded self-perception within a narrative of nature experiences. At the neural level, the DI computed between resting-state and cognitive trance was higher than the empirical cut-off (Casarotto et al., 2010), both during frontal and parietal sessions, though particularly pronounced in the latter. This is consistent with the findings observed in Bodart et al. (2018). Moreover, during the trance state, there was an increase in the amplitude of TEPs during frontal stimulation, contrasting with a decrease during parietal stimulation, as also indicated by the amplitude of local mean field power (LMFP). Further, frontal stimulation elicited a broad-band enhancement of local PLF and power (assessed with the event-related spectral perturbation; ERSP) during trance compared to the resting state, whereas parietal stimulation resulted in an early decline in PLF without a significant alteration in power. Therefore, in summary, all examined TMS-EEG indicators in this study (i.e., TEP, LMFP, ERSP and PLF) were heightened compared to resting state during cognitive trance when stimulation was administered over the frontal area, while most measures showed a decline during parietal stimulation (i.e. LMFP and local PLF). These data suggest a marked target-specific dissociation of TMS-EEG neurophysiological measures. The investigators hypothesized that the amplified frontal responses could be attributed to changes in attention, internal monitoring, and mental imagery. Conversely, the diminished parietal responses could potentially relate to lower consciousness of the environment.

Other studies have integrated neuromodulation with brain activity measurements to further explore specific components of certain types of meditation, such as self-compassion. Luo et al. (2023) used iTBS within a TMS-EEG procedure to investigate relations among self-compassion and DLPFC dynamics. Here, a cohort of thirty-two individuals underwent either iTBS or sham targeting the L-DLPFC (using F3 as reference) while they were instructed to either engage in self-compassion strategies or to experience a scenario of social rejection. Behaviorally, there was a significant increase in self-reported self-compassion among participants when underwent iTBS condition compared to sham. At the neural level, iTBS, as compared to sham, led to heightened gamma power across frontal and centro-parietal brain regions during engagement in self-compassion. Moreover, there was an enhancement in frontal and central gamma band synchronicity following iTBS during self-compassion. Importantly, increased gamma power and coherence were positively associated with self-compassion engagement in the iTBS condition. In addition, iTBS showed opposite effects on theta activity depending on the social context: self-compassion decreased frontal theta activity, while social rejection enhanced it. Moreover, theta band coherence increased following iTBS in both conditions. In the self-compassion condition, this increase occurred within frontal and

fronto-occipital areas. These results suggest a critical role of the DLPFC in shaping the experience of self-compassion with gamma band power and coherence being particularly linked to it, while theta activity appears to be less specific. Notably, these findings support earlier studies of loving-kindness and compassion meditation practices that also found the involvement of gamma power in this form of meditation (Lutz et al., 2004). Yet, other studies have also found that mindfulness meditation is associated with gamma power supporting attention and sensation integration (e.g., Berkovich-Ohana et al., 2012). Therefore, the inquiry remains whether this frequency band is exclusively specific to these meditation forms or if it represents a broader meditation phenomenon.

Other investigations have further explored the effects of TMS protocols on meditation. However, these studies have thus far, to the best of our knowledge, not incorporated neuroimaging or neurophysiological techniques to examine its neurobiological effects (e.g., Cavallero et al., 2021). Therefore, while such investigations are relevant to the broader context of TMS and meditative practices, they fall outside the scope of the present article.

10. Insights derived from combining neuromodulation and meditation

In the prior section, we reviewed six studies (Bodart et al., 2018; Gosseries et al., 2020; Hunter et al., 2018; Luo et al., 2023; Nishida et al., 2021; Sefat et al., 2022). All these studies used EEG to explore brain dynamics; notably, none employed fMRI. Meditation contexts varied widely, including mindfulness (Hunter et al., 2018; Nishida et al., 2021) and yoga interventions (Sefat et al., 2022), volitionally induced mental states in long-term practitioners (Bodart et al., 2018; Gosseries et al., 2020), and specific meditation-related strategies as self-compassion (Luo et al., 2023). In terms of neuromodulation techniques, the three studies that employed tES procedures, all utilized tDCS protocols (Hunter et al., 2018; Nishida et al., 2021; Sefat et al., 2022). Among the TMS investigations, two used single-pulse TMS protocols (Bodart et al., 2018; Gosseries et al., 2020) and only one used rTMS (iTBS; Luo et al., 2023). The neuromodulation targets in all cases were primarily frontal, either in isolation (Hunter et al., 2018; Luo et al., 2023; Nishida et al., 2021; Sefat et al., 2022) or in combination with parietal stimulation (Bodart et al., 2018; Gosseries et al., 2020).

At the behavioral level, both cognitive (i.e., working memory; Hunter et al., 2018) and affective domains (i.e., anxiety; Nishida et al., 2021) were ameliorated with the combined use of neuromodulation and meditation interventions. Furthermore, dissociative effects in frontal and parietal stimulation were observed in self-reports of long-term meditators (e.g., see distinct frontal and parietal VAS responses during trance in Gosseries et al., 2020). Moreover, rTMS increased self-compassion compared to sham (Luo et al., 2023). These results are in line with previous reviews reporting behavioral and clinical enhancements of these types of combined interventions (i.e., Divarco et al., 2023; Rebello-Sanchez et al., 2022). However, none of the studies utilized neuromodulation strategies directly perturbing phenomenological processes during meditation, which may have been particularly relevant, especially in the studies with long-term meditators.

At the neural level, Hunter et al. (2018) observed a fronto-parietal dissociation, characterized by a decrease in frontal and an increase in parietal P3 amplitude and theta power following tDCS stimulation. Further, Nishida et al. (2021) reported a reduction in alpha activity in the L-DLPFC and rACC in the tDCS group compared to sham. Finally, Sefat et al. (2022) identified connectivity changes predominantly within the fronto-parietal areas. Further, TMS-EEG responses exhibited distinctive frontal and parietal response patterns in each self-induced mental state of long-term meditators: open presence monitoring increased TMS-related responses in both frontal and parietal targets, while the drowsy state was associated with decreases in both target responses. SICO was associated with frontal decreased but parietal increased TMS-EEG reactivity, while the cognitive trance state showed a

pattern of increased frontal but decreased parietal TMS-EEG reactivity and phase locking responses. Interestingly, authors interpreted the neural TMS responses in these self-induced mental states within the context of the state's corresponding phenomenological effects (Bodart et al., 2018; Gosseries et al., 2020). Finally, Luo et al. (2023) mainly demonstrated rTMS-induced increases in gamma power and coherence across frontal, central, and centro-parietal regions during self-compassion. Further, theta modulations were detected depending on the social context. Importantly, in the reviewed articles, neural changes were occasionally individually associated with the induced behavioral modifications. These studies are particularly relevant for understanding the neural mechanisms underlying the observed behavioral changes resulting from combined neuromodulation-meditation interventions (i.e., Hunter et al., 2018; Luo et al., 2023; Nishida et al., 2021). Moreover, this data also aids in understanding the neurobiological processes related to distinct meditative states (Bodart et al., 2018; Gosseries et al., 2020).

In summary, different brain regions have been implicated in the reviewed findings, particularly emphasizing the dynamics of the frontal and fronto-parietal circuitry (e.g., Bodart et al., 2018; Gosseries et al., 2020; Hunter et al., 2018; Luo et al., 2023; Sefat et al., 2022). More precisely, specific frontal and parietal patterns in the P3 amplitude and power of theta have been reported when using tDCS in combination with mindfulness meditation (Hunter et al., 2018). Furthermore, in long-term meditators during advanced meditation practice, frontal and parietal modulations in specific oscillatory frequencies have been linked to distinct self-induced mental states, including changes in natural frequencies that are specific to the stimulated targets (e.g., beta band oscillations [15–25 Hz] within the parietal cortex and fast beta/gamma-band oscillations [25–35 Hz] in the premotor cortex; Bodart et al., 2018). Moreover, increases in gamma power and coherence in the frontal and parietal cortices have also been observed in response to iTBS (Luo et al., 2023). In addition, a decrease in alpha activity post-tDCS entailing frontal and cingulate areas have also been reported (Nishida et al., 2021). Altogether, these findings are largely consistent, at the topographical level, with descriptive neuroimaging data underscoring the significance of the frontal, parietal, and fronto-parietal areas in meditation (e.g., Fox et al., 2014a; 2016). At the neurophysiological level, data is also partially consistent with previous descriptive evidence highlighting the role of alpha (Lomas et al., 2015), gamma (Lutz et al., 2004) and theta oscillations (Lomas et al., 2015; Yordanova et al., 2021) in distinct meditation modalities. Regarding brain-behavioral hypothesis and models, the reported results (i.e., Hunter et al., 2018) are consistent with previous data indicating that meditation may increase cognitive function (i.e., Chételat et al., 2017; Gard et al., 2014). This enhancement may be neurobiologically explained through the neural efficiency hypothesis, supposedly facilitated when implementing neuromodulation in combination with meditation (e.g., Hunter et al., 2018). Additionally, part of the reviewed studies (i.e., Nishida et al., 2021) support findings that indicate that meditation effectively decreases psychopathological symptomatology (i.e., Galante et al., 2023a; Goldberg et al., 2018; Kuyken et al., 2016). These emotional changes might be explained through the engagement of top-down inhibitory processes (e.g., Brefczynski-Lewis et al., 2007)—in Nishida et al. (2021) potentially encompassing prefrontal, cingulate and possibly limbic connections.

Nevertheless, several constraints are present here. First, in certain instances, the control group was non-equivalent (Hunter et al., 2018), which limits our interpretation of the results. Further, in some cases, it is challenging to discern whether the reported outcomes are attributable to the combined intervention or represent effects related to either the neuromodulation or meditation components individually (i.e., Luo et al., 2023). Moreover, although Bodart et al. (2018) and Gosseries et al. (2020) applied similar TMS-EEG protocols, they were applied in distinct hemispheres, which might implicate important differences (i.e., Kurth et al., 2015b). Furthermore, these case studies with long-term

meditation practitioners compared the stimulation effects only with baseline states, while sham conditions were absent. This does not allow us to comprehend if neuromodulation potentiated the effects of meditation, as it is only able to reveal topographical frontal-parietal dissociations in the distinct self-induced explored states. Additionally, even though observed behavioral and neural effects at the frontal and fronto-parietal cortical regions might be genuine, they might also be highly related to the stimulation targets and neurophysiological procedures used to explore brain responses (i.e., EEG). In addition, it is difficult to determine, in specific cases, whether reported neural outcomes represent actual mechanisms driving behavior or if they are instead predictors of behavioral change (Nishida et al., 2021). Further, while some of the neuromodulation findings align with prior neurophysiological descriptive studies, discrepancies emerge when examining specific outcomes between long-term meditators and novices (i.e., only gamma involvement may link both neuromodulation and descriptive studies in long-term practitioners, i.e., Bodart et al., 2018; Lutz et al., 2004). What's more, it proves challenging to reconcile certain observed neuromodulation results (i.e., the implication of rACC in combined neuromodulation and meditation protocols: Nishida et al., 2021) with specific theoretical and network models elucidated in previous descriptive meditation investigations (i.e., top-down processes: Brefczynski-Lewis et al., 2007; relevance of ACC and SN: Hölzel et al., 2007). Finally, despite reviewed studies reporting apparent facilitations of both behavioral and neural effects when neuromodulation was combined with meditation, none of the reviewed studies were designed to induce a virtual lesion to perturb neural activity associated with a particular meditation process. As mentioned, this approach could potentially contribute significantly to the delineation of causal links between brain function and behavioral outcomes in meditation research.

11. Integrating previous neuromodulation studies with the neuroscience of meditation

The dynamics of the DMN have been consistently associated with meditation (e.g., Brewer et al., 2011; Fox et al., 2016; Fujino et al., 2018; Garrison et al., 2015). However, the central components of this network have not yet been directly targeted with NIBS in the context of meditation. This approach holds considerable promise, especially given the success of previous neuromodulation studies that effectively targeted and modulated this brain network. Particularly, studies demonstrated feasible modulation of the DMN's central hubs, including the mPFC and PCC/PCU, both of which are directly implicated in meditation. These brain stimulation studies employed varied stimulation procedures, including the application of rTMS to accessible DMN nodes, such as the IPL (Abellana-Pérez et al., 2019; Eldaief et al., 2011; Vidal-Piñero et al., 2015). Remarkably, these neuromodulation investigations have shown results at the topographical level that bear noticeable resemblance to those observed in descriptive meditation imaging studies. For instance, upon close examination of Fig. 3 C in Eldaief et al. (2011) alongside Fig. 1 in Brewer et al. (2011), it becomes evident that there is significant overlap between the regions influenced by NIBS (Eldaief et al., 2011) and those observed in long-term practitioners during meditation (Brewer et al., 2011).

To date, only one study on meditation has successfully modulated brain regions classically involved within the SN using NIBS, such as the ACC (Nishida et al., 2021). Nonetheless, other nodes within the SN—like the insula, which has been previously linked to meditation in both structural and functional studies (Falcone and Jerram, 2018; Fox et al., 2014a; 2016)—have not yet been externally modulated with NIBS in meditation contexts. Despite the inherent complexity arising from the depth of the SN primary nodes (i.e., ACC and insular cortices), prior brain stimulation studies have attempted to modulate this network. In this context, deep rTMS techniques, such as those involving specialized coils (e.g., H7 or double-cone coils) have been used to reach these profound regions (i.e., Cheng et al., 2023; Kreuzer et al., 2015). For

example, [Perini et al. \(2020\)](#) applied a deep rTMS protocol in a cohort of treatment-seeking alcohol-dependent individuals, targeting the insular cortex bilaterally. Although no significant clinical outcomes were observed, end-of-treatment seed-based resting-state functional connectivity (rs-FC) analysis of the insula revealed neural differences between the active rTMS and sham groups. Specifically, the study revealed decreased connectivity between the right posterior insula and left precuneus in the rTMS group compared to sham. Conversely, increased connectivity between the left posterior insula and right posterior cingulate was observed in the rTMS group as compared to sham. These findings suggest that rTMS may induce alterations in insular functional connectivity, although these alterations might not always translate into behavioral changes. This could potentially be attributed to the partial engagement of insular dynamics with rTMS or an insufficient intensity of stimulation. Nonetheless, this data underscores the potential of non-invasive neuromodulation techniques in modulating the functioning of the insular cortex. Additional studies have also employed simulation methodologies to investigate optimal tDCS montages for effectively modulating the insular cortices (i.e., [Esmaeilzadeh Kiabani et al., 2023](#)). It is also noteworthy that beyond the direct targeting of specific subcortical regions, it is plausible to modulate deep structures by targeting functionally interconnected cortical areas (i.e., [Fox et al., 2014b](#)). This indirect modulation is likely what occurred in the previously described study by [Nishida et al. \(2021\)](#). Indeed, [Nishida et al. \(2021\)](#) results might be elucidated in the context of data reported by [Vink et al. \(2018\)](#), which applied single-pulse TMS to the left DLPFC in ten healthy individuals using a concurrent TMS-fMRI setup. In this study, they observed that DLPFC stimulation triggered activity in various brain regions connected to the DLPFC, including regions of the ACC. Hence, [Vink et al. \(2018\)](#) study provides relevant evidence of NIBS-induced activity propagating from the DLPFC to deeper structures, such as the ACC, and supports the potential of NIBS for directly modulating ACC-related regions and possibly other areas connected to these structures.

The approach of modulating subcortical structures by targeting connected cortical areas has also been used, in other contexts, for influencing profound limbic regions, as the hippocampus or the amygdala. For example, [Wang et al. \(2014\)](#) implemented a high-frequency rTMS protocol to investigate whether the modulation of cortico-hippocampal pathways could enhance the strength of these functional connections and thereby induce memory improvements. In this study, the stimulation target was personalized for each subject, identified using resting-state fMRI to select a left lateral parietal region with high functional connectivity to the left hippocampus. On the one hand, the behavioral results indicated enhanced cognitive performance following rTMS intervention compared to the control condition. On the other hand, results showed a pronounced increase in functional connectivity within the targeted cortico-hippocampal loops. Remarkably, this enhancement of functional connectivity was correlated, at the individual level, with the rTMS-related increase in memory performance. In another related study, [Sydnor et al. \(2022\)](#) combined TMS with fMRI to investigate how TMS applied to the ventrolateral prefrontal cortex (vlPFC) may affect the activity of the amygdala. The results indicated that TMS was related to acute and localized neural activity changes in the amygdala. Notably, the magnitude of these changes was correlated with the density of white matter pathways connecting the vlPFC and the amygdala. Hence, both the findings from [Wang et al. \(2014\)](#) and [Sydnor et al. \(2022\)](#) underscore TMS's potential to influence subcortical neural activity through neuroanatomically meaningful cortico-subcortical functional or structural connections. It is also worth highlighting that more recently developed neuromodulation techniques, including transcranial focused ultrasound (tFUS; [Dell'Italia et al., 2022](#); [Zhang et al., 2021](#)) and transcranial temporal interference stimulation (tTIS; [Grossman et al., 2017](#); [Wessel et al., 2023](#)), hold potential for non-invasively stimulating deep and small structures in the brain.

Finally, the role of fronto-parietal circuits in meditation has been

elucidated through brain imaging studies ([Brefczynski-Lewis et al., 2007](#); [Kajimura et al., 2020](#)). In addition, previous descriptive research has also focused into the neural oscillations within this fronto-parietal system during meditation, consistently implicating alpha and theta bands in mindfulness meditation ([Lomas et al., 2015](#)). Moreover, in long-term meditators, the significance of theta ([Yordanova et al., 2021](#)) and gamma band frequencies ([Lutz et al., 2004](#)) has also been highlighted. Studies integrating brain stimulation techniques in meditation contexts have revealed the involvement of a broad-spectrum of frequencies in frontal and parietal regions, including theta ([Hunter et al., 2018](#); [Luo et al., 2023](#)), gamma ([Bodart et al., 2018](#); [Luo et al., 2023](#)), alpha ([Nishida et al., 2021](#)) and beta ([Bodart et al., 2018](#)). However, the causal implications of these frequency bands in meditation (or in specific meditation modalities) remains unknown. To elucidate these types of uncertainties, prior scientific research has used neuromodulation protocols, particularly perturbation approaches. In this vein, in a well-designed investigation conducted by [Polanfa et al. \(2012\)](#), tACS was applied at theta frequencies targeting the frontal and parietal nodes of the FPN. Three stimulation conditions were implemented: a synchronized condition (0° phase difference), a desynchronized condition (180° phase difference), and a sham stimulation condition. These conditions were applied while participants performed a working memory task. The results revealed that externally induced fronto-parietal theta synchronization enhanced performance (reaction times) in contrast to the sham group. Conversely, induced fronto-parietal theta desynchronization resulted in a decrement in cognitive performance compared to sham. This study bears considerable relevance as it pioneers the establishment of a causal link between specific oscillatory activities across concrete cortical areas and cognitive performance in healthy human subjects. This investigation is relevant in the meditation arena because the theta band appears to be a convergent neural feature found in both descriptive meditation studies ([Lomas et al., 2015](#); [Yordanova et al., 2021](#)) and combined neuromodulation-meditation studies ([Hunter et al., 2018](#); [Luo et al., 2023](#)). However, research has yet to causally elucidate the implication of the theta band (and the other bands as well) in meditative practice.

12. New opportunities for combining neuromodulation and meditation

In this article, our focus has been on outlining the initial research efforts aimed at elucidating the neural substrates beyond combined neuromodulation and meditation procedures. These studies are crucial in identifying distinct modifiable neural features engaged in the meditation process. Such insights could potentially serve to effectively guide brain stimulation techniques to modulate distinct processes across different meditation contexts. Here, the procedures delineated in the preceding section might be considered as research models for applying novel investigation approaches in meditation settings. These NIBS-based protocols can be applied both during the meditation process (i.e., online stimulation) or before/after (i.e., offline neuromodulation procedures). Furthermore, the goal of these stimulation protocols may not only be improving behavioral (i.e., [Hunter et al., 2018](#); [Luo et al., 2023](#); [Nishida et al., 2021](#)) or neural meditation effects (i.e., [Sefat et al., 2022](#)) but can also be applied as perturbation procedures, disrupting key brain dynamics linked to meditation and thereby leveraging their potential for deriving brain-behavior causal attributions in human research. Additionally, these brain stimulation techniques do not necessarily focus solely on modulating a specific target associated with meditation. Instead, considering the various mental processes and neural features engaged in distinct meditation modalities, it may be feasible to modulate different brain systems depending on the specific processes aimed to be modulated in each context. In this vein, it would even be conceivable to specifically modulate distinct neural networks in a concurrent manner, such as increasing the SN activity (mainly related to attentional processes) while concomitantly attenuating the DMN (principally linked

to self-awareness). In this context, multifocal stimulation protocols could be employed (i.e., Fischer et al., 2017). Relatedly, we recently investigated the possibility of using an online multifocal tDCS protocol combined with fMRI to induce complex brain activity patterns. Specifically, our focus was on enhancing activity within the FPN while concurrently reducing activity in areas associated with the DMN. Results from this research effort highlighted that these network-based stimulation paradigms are feasible for modifying brain activity and connectivity on a large-scale manner (see for further detail Abellana-Pérez et al., 2021; Vaqué-Alcázar et al., 2021). Furthermore, these neural features might also be theoretically modulated in a time-dependent manner. Therefore, it would be possible to allocate the initial phase of the meditation session to one target and subsequently transition the stimulation to another one. In this context, it is also worth noting that employing neurofeedback or closed-loop methodologies could enable the adjustment of neuromodulation parameters in response to real-time brain signals (i.e., Guleken et al., 2020; Scangos et al., 2021; Soleimani et al., 2023). In this context, it is worth noting that while current evidence indicates that combining meditation-based interventions with NIBS can enhance cognitive and affective outcomes in healthy individuals (e.g., Hunter et al., 2018; Nishida et al., 2021), integrating such methodological advancements into these procedures holds substantial potential for further improving their effectiveness. Furthermore, beyond promoting well-being in healthy individuals, these research avenues suggest promise for therapeutic applications. For instance, meditation-based interventions have demonstrated benefits for neurological disorders such as Parkinson's disease (e.g., Lin et al., 2023) and psychiatric conditions including addiction (e.g., Garland and Howard, 2018). Nonetheless, results from studies combining NIBS with meditation procedures in these contexts have been modest (e.g., Park et al., 2021). To address these limitations, we propose optimizing and personalizing neuromodulation protocols. This approach may involve personalizing the targeting of brain networks and neural oscillations, along with dynamically adjusting stimulation parameters. These individually-tailored interventions promise to accelerate meditation-related benefits for well-being, and improve symptoms in clinical populations.

Moreover, NIBS methodologies are also powerful tools for eliciting and evaluating different features of brain plasticity, which refers to the inherent capacity of the nervous system to undergo structural and functional modifications in response to internal or external demands (Freitas et al., 2011; 2013; Jannati et al., 2023; Pascual-Leone et al., 2005). Prior studies have highlighted hypo- or hyper-plasticity as mechanisms underlying numerous brain health conditions (i.e., including autism spectrum disorder and AD; Jannati et al., 2023 and Pascual-Leone et al., 2011). Additionally, NIBS-inducing plasticity procedures (i.e., TBS protocols) have demonstrated usefulness for investigating plasticity beyond the specific targeted region, encompassing its corresponding brain networks. Indeed, in a previous study, we observed that younger and older adults respond differently to the same plasticity-inducing rTMS protocol at the large-scale network level. Specifically, following iTBS over the lIPL, younger adults exhibited an increase in rs-FC in distal areas within the DMN (i.e., frontal DMN nodes). In contrast, older adults exhibited increases in rs-FC in proximal DMN regions emanating from the stimulated region (i.e., PCC). Furthermore, we noticed that some older adults retained the ability to respond to iTBS in a long-range manner, mirroring the neural iTBS responses observed in younger adults. These individuals were categorized as older adults 'young-like' responders. Interestingly, this subgroup of older participants displayed greater functional and structural brain integrity, as evidenced by DMN long-range and hippocampal connectivity as well as fractional anisotropy measures. Older adults with 'young-like' responses also had higher cognitive reserve and better cognitive performance both at baseline (pre-iTBS) and during a 3-year follow-up, compared to older adults with 'non-young-like' iTBS-induced responses. These relationships were not evident when

considering baseline fMRI data (i.e., before stimulation). Therefore, this study suggests that iTBS-induced responses in brain networks (i.e., network plasticity) may be a closer indicator for brain integrity and cognitive phenotype than baseline brain imaging measures (Abellana-Pérez et al., 2019). Nonetheless, the extent to which meditation influences distinct plasticity processes remains understudied. It is plausible to theorize that differential meditation-centered interventions may induce distinct observable modifications in brain plasticity mechanisms. Additionally, whether higher levels of expertise in meditation (including the capacity to access profound states of mind, i.e., Chowdhury et al., 2023; Ganesan et al., 2024; van Lutterveld et al., 2024; Yang et al., 2023; 2024) may also be associated with specific neuroplastic processes, remain similarly understudied. In both scenarios, neuromodulation methodologies could be employed to thoroughly investigate in what manner plasticity can be influenced through meditation training and expertise, and whether self-induced alterations in conscious experience are inherently linked to identifiable brain plasticity processes.

Further from the neuromodulation procedures aimed to induce plasticity processes, it is worth highlighting that single and paired-pulse TMS responses have also facilitated the differentiation between distinct clinical phenotypes. In this context, paired-pulse TMS protocols have been employed to investigate short-interval intracortical inhibition and facilitation, long-interval intracortical inhibition, and short-latency afferent inhibition (i.e., Benussi et al., 2017; Padovani et al., 2018). These studies demonstrate that TMS has high sensitivity and specificity for distinguishing AD from frontotemporal dementia (FTD) and healthy controls (Benussi et al., 2017). Similarly, Padovani et al. (2018) demonstrated the efficacy of paired-pulse TMS metrics in enhancing the characterization of distinct mild cognitive impairment (MCI) subtypes, specifically distinguishing MCI due to AD and MCI not due to AD. Therefore, TMS can serve as a non-invasive and cost-effective screening tool for the differential diagnosis of certain neurologic conditions including MCI, FTD and AD (Benussi et al., 2017; Padovani et al., 2018). Additional investigations have also revealed that single-pulse TMS-evoked responses, as captured by EEG recordings and compared to baseline electrophysiological data, could provide meaningful indices for delineating specific cortical excitability profiles and associated behaviors. These metrics might serve as valuable markers for distinguishing various typologies among neurological patients, such as epilepsy (Shafi et al., 2015). Likewise, in a study of a cohort of healthy individuals (Cattaneo et al., 2018), we observed distinct patterns in single-pulse TMS-EEG responses over the L-DLPFC associated with various mental health trajectories during a stressor event, in this case the COVID-19 lockdown. Specifically, individuals who showed heightened mental distress (considered vulnerable individuals) during the pandemic lockdown demonstrated significantly larger late EEG responses following L-DLPFC stimulation compared to those who maintained stable mental health (identified as resilient subjects) prior to the pandemic's onset. In other words, individuals with higher psychological resilience to COVID-19 lockdown showed brain patterns that were more resistant to modulation by an external TMS perturbation. Notably, these opposing mental health trajectories were not discerned solely based on baseline EEG recordings. Therefore, these findings underscore the potential of TMS-induced brain responses to provide unique insights (Perellón-Alfonso et al., 2022; see also Pascual-Leone and Bartrés-Faz, 2021). Note that both studies by Abellana-Pérez et al. (2019) and Perellón-Alfonso (2022) emphasize that modulating brain dynamics with NIBS introduces a layer of complexity, further from baseline (or pre-stimulation) data, in understanding the brain function. This approach holds the potential to bring us closer to the individual phenotype, both regarding cognitive performance and mental health status, as compared to baseline MRI or EEG data. In the context of meditation, as denoted by Tang et al. (2015), individuals may not uniformly respond to distinct meditation interventions. Therefore, such previously described brain markers (i.e., Padovani et al., 2018; Shafi

et al., 2015) that leverage individual responses to NIBS procedures (i.e., Hamada et al., 2013; López-Alonso et al., 2014; Nettekoven et al., 2015) to aid in brain characterization, might similarly be used in the context of meditation-based treatments. Indeed, these procedures could potentially advance the implementation of personalized medicine principles within meditation settings (see also Rebello-Sanchez et al., 2022). Moreover, the extent to which meditators exhibit TMS-related resilience metrics remains unstudied. This is particularly relevant given previous research suggesting meditation may foster psychological resilience (e.g., Kwak et al., 2019). Building upon the findings of Perellón-Alfonso et al. (2022), it becomes intriguing to investigate whether long-term meditators—particularly during advanced meditative states—exhibit heightened resilience estimates to externally-induced perturbations. Further, it is also relevant to elucidate if these resilience-like responses could be modulated during a meditation intervention. Conducting such studies would not only advance our understanding of the neural mechanisms underlying meditation, but also shed light on how meditation contributes to the development of resilience.

13. Conclusions

Our current understanding of the neuroscience of meditation is evolving. However, the mechanistic underpinnings of meditation remain only partially understood. In this review, we present pioneering research studies that have combined neuromodulation with meditation while also revealing associated neural data. These studies have mainly aimed to boost, with the use of distinct stimulation protocols, the behavioral and neural effects induced by meditation interventions (i.e., Hunter et al., 2018; Luo et al., 2023; Nishida et al., 2021; Sefat et al., 2022), as well as to test cortical responsiveness linked to distinct meditative states (i.e., Bodart et al., 2018; Gosseries et al., 2020). Neuromodulation protocols in this context have mainly focused on targeting frontal and parietal brain regions (i.e., Bodart et al., 2018; Gosseries et al., 2020; Hunter et al., 2018; Luo et al., 2023; Sefat et al., 2022). The outcomes have primarily revealed the implication of fronto-parietal loops in distinct meditation contexts (i.e., Hunter et al., 2018; Luo et al., 2023; Sefat et al., 2022), as well as the specific significance of frontal and parietal areas in distinct self-induced mental states (i.e., Bodart et al., 2018; Gosseries et al., 2020). Notably, only one study included in the review was able to modulate SN-related nodes (Nishida et al., 2021). However, no single study has attempted to specifically target brain areas related to the DMN and the cortico-limbic system while also reporting the neurobiological outputs obtained. Furthermore, no single study has intended to directly modulate any specific neural frequency previously linked to meditation practice (i.e., with the use of tACS). Extending beyond these specific points, it remains to be demonstrated the causal implication of the described neural features in meditation with well-designed and perturbation-based protocols. Furthermore, the influence of plasticity mechanisms within this context requires further investigation and clarification. To overcome inherent limitations of previous studies, progress in this domain necessitates a stronger integration of descriptive neurobiological models with the strategic use of neuromodulation techniques, leveraging all the possibilities they might offer in this context. From our perspective, the present moment presents an ideal opportunity to initiate this venture, which holds the promise of enhancing our mechanistic neurobiological comprehension of meditation. Ultimately, this scientific knowledge is essential for optimizing meditation-based interventions aimed at improving human health, well-being, and resilience in all types of populations.

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Conflict of Interest

A.P.-L. is listed as an inventor on several issued and pending patents on the real-time integration of transcranial magnetic stimulation with electroencephalography and magnetic resonance imaging, and applications of noninvasive brain stimulation in various neurological disorders; as well as digital biomarkers of cognition and digital assessments for early diagnosis of dementia. He is a co-founder of Linus Health and TI Solutions AG and serves on the scientific advisory boards for Starlab Neuroscience, Magstim Inc., MedRhythms, TetraNeuron, and Skin2-Neuron. None of these companies have any interest in or have contributed to the present work. The remaining authors declare that they have no competing interests.

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